A MULTI-SCALE STUDY ON THE MOVEMENT ECOLOGY OF AFROTROPICAL WATERBIRDS

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This thesis is dedicated to my father, Richard Dominic Wilmot Henry (1940-2008).

"The movement of animals that belong to each genus, and how these are differentiated, and what the reasons are for the accidental characteristics of each…all this we have considered elsewhere. But now we must consider in general the common reason for moving with any movement whatsoever - for some animals move by flying, some by swimming, some by stepping, some in other comparable ways"

Aristotle 330 BC

De Motu Animalium (On the movement of animals)

DECLARATION

This thesis is the result of my own work and, except where indicated by specific reference in the text, contains no work in collaboration with others. The text does not exceed 80,000 words. It has not been previously submitted, in part or whole, to any university or institution for any degree, diploma, or other qualification.

Signed: 

Date: 28/07/2015

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ABSTRACT

Understanding the processes and mechanisms governing animal movement is a fundamental goal in ecology. Processes driving movement can occur across multiple spatiotemporal scales and have important consequences for the structure and dynamics of populations, communities and ecosystems. The study of movement provides insights into the ecological resources and habitats necessary for persistence of species and communities. It also provides a theoretical and applied basis from which to formulate informed conservation plans. Waterbirds in semi-arid southern Africa are an ideal study group for understanding interactions between movement and environmental factors because they exhibit a wide range of movement strategies and are located within a landscape in which resources are characterised by high levels of spatiotemporal variability. Emphasis has been placed on understanding movement phenomena from individually-tracked animals, but cases which consider this approach in conjunction with traditional community ecology perspectives are rare. In this thesis I explored questions of movement in both individuals and communities, and argue that an integrated multi-scale approach is necessary to advance our broader understanding of movement in waterbirds.

In the first part of the study I addressed an individual-level movement perspective. I used fine-scale telemetry data from 35 individually tracked Egyptian Geese *Alopochen aegyptiaca* and Red-billed Teal *Anas erythrorhyncha* with novel analytical techniques to explore questions of trade-offs in habitat selection, functional responses and whether movement responses to landscape resources are reactive or prescient. My findings suggested that, at the home-range scale, both forage optimisation and predation risk were limiting factors of movement and habitat selection of Egyptian Geese. I also showed for the first time that waterbirds exhibit functional responses in relation to changes in the availability of habitat types. I subsequently showed that the proximate drivers of waterfowl movement are the dynamics of rainfall and primary productivity. Egyptian Geese and Red-billed Teal were able to perceive and respond to temporal shifts in resource conditions prior to habitat patch occupation. This in turn suggested that their movements in semi-arid landscapes are underpinned by an intimate knowledge of the local environment and that waterfowl exhibit a complex behavioural movement strategy.

In the second part of the study I used waterbird count data collected from wetlands in KwaZulu-Natal, South Africa, to address the community-level movement perspective.

Using novel multivariate techniques I explored the role of movement and spatial scale in defining ecological niches of waterbirds. I also tested the relative importance of spatial and environmental processes in structuring waterbird metacommunities, and how these processes vary over time. My results suggested that the scale of landscape resources can act as a filter of movement traits and waterbirds with different movement capacities can occupy distinct ecological niches. Waterbird metacommunities were primarily structured by species sorting mechanisms, however, spatial processes did play a significant role in shaping communities. Metacommunity processes showed temporal variation through the study period, suggesting that stable community structuring mechanisms cannot always be detected using a single sampling period.

The majority of our understanding of waterbird ecology is based on studies conducted in northern hemisphere systems, and so this thesis makes a novel contribution to understanding movement in systems where waterbirds face a contrasting set of landscape resource constraints. By combining telemetry data and environmental data over broad spatiotemporal scales, I showed that waterbirds pursue a complex behavioural strategy to adapt to landscapes characterised by high levels of resource uncertainty. My findings revealed the importance of rainfall and primary productivity as environmental drivers of waterbird movement in arid landscapes. Through adopting a community-level perspective I also demonstrated the importance of movement in structuring metacommunities and the role it plays in determining the ecological niches of waterbirds. Movement is a complex phenomenon; developing frameworks that consider movement at multiple levels of biological organisation and across multiple spatiotemporal scales will enhance our ability to effectively understand movement processes in a holistic manner.

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To my good friends, Grant Gardner, Brent Jachs and JP du Buisson, who still aren't really sure what I do. I hope you read the executive summary (we call it an abstract which, in

the classical sense of the word, it is anything but) and look at the pictures to get a sense of what I've been occupied with over the last few years. Thank you all for your friendship.

My deep appreciation goes to my family: Mom, Emma and Justin. Thank you for your unending love, support and prayers, and especially for always believing in me. You have all shared in my trials and tribulations and I couldn't have done it without you. I love coming home to the farm for a bit of respite and feeling like I never left. Justin, you have been a brother in the truest sense of the word. Thank you for joining me in the field and especially for all the help sorting out the various vehicle & logistical crises.

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WETLAND
WATERBIRD
ENVIRONMENTAL
MOVEMENT
HABITAT
FUNCTIONAL
SELECTION
SPECIES
MODEL
VEGETATION
BIRDS
FORAGING
VARIANCE
RAINFALL
SPATIAL
SCALE
RANGE
LANDSCAPE
ANALYSIS
PATTERNS
QUALITY
STRUCTURE
SEASON
GEESE
EGYPTIAN
RESOURCES
TRAITS
COMMUNITIES
RESPONSE
WATER
INDIVIDUAL
POPULATIONS
ECOLOGICAL
UNDERSTANDING
FRACTION
AFRICAN
VARIATION
SIGNIFICANT
SOUTHERN
NOMADIC
TEAL
DYNAMICS
DISTANCE
PROCESSES
CONDITIONS
MIGRANTS
ANIMALS
CLUSTER
INCREASED
TEMPORAL
NATURAL
CULTIVATED
WATERFOWL
FLOODPLAIN
RESIDENTS
FOLLOWING
METACOMMUNITY
AFRICA
BEHAVIOUR
LOCAL
GROUPS
HOME
PARAMETER
ALLOWED
COUNTS

CONTENTS

LIST OF ABBREVIATIONS

AIC	Akaike information criterion
ANTHRO	Anthropogenically modified land cover
AQ-FG	Aquatic flooded grass
AQ-RS	Aquatic reeds and sedges
AQ-SF	Emergent vegetation (soft stemmed plants), submerged vegetation and floating vegetation
ARS	Area-restricted search
BAR	Barberspan
CARN	Carnivorous
CM	Connectivity matrix
CULT	Cultivated land cover
CWAC	Coordinated Waterbird Counts
DEEP	Species that forage over or in deep water
DEGR	degraded land cover
DO	Dissolved oxygen
EG	Egyptian Goose
Elev	Elevation
EMERGE	Species that forage in emergent vegetation including reeds and other macrophytes
FPT	First-passage time
GWH	Green Wave Hypothesis
HERB	Herbivore
IBA	Important Bird Area
Inter.M	Inter-African migrant

Intra.M	Intra-African migrant
INVERT	Invertebrates
JOZ	Jozini Dam
MAN	Lake Manyame
ME	Mass effects
MEM	Moran's Eigenvector Maps
MKDE	Movement-based Kernel Density Estimator
mNDWI	Modified normalised difference water index
NAT(NATU)	Natural vegetation
NDVI	Normalised difference vegetation Index
NLC	National Land Cover
NM	Neutral model
PD	Patch dynamics
PE	Purely environmental
Precip	Rainfall
PS	Purely spatial
PTT	Platform transmitter terminal
RBT	Red-billed Teal
RDA	Redundancy analysis
RLQ	R-mode linked to Q-mode
RSFs	Resource-selection functions
SAFRING	South African Bird Ringing Unit
Sal	Salinity
SHALLOW	Species that forage in shallow water
SHORT	Species that forage in short vegetation, grass or mudflats
SL – GM	Shoreline grass and mudflats

SL – RS	Shoreline reeds and sedges
SL – TS	Trees and shrubs
SS	Species sorting
SSE	Spatially structured environmental
STR	Strandfontein
SWM	Spatial-weighting matrix
Temp	Temperature
URBA	Urban-built up land cover
WET(WETL)	Estuarine and freshwater cover
WM	Weighting matrix

LIST OF TABLES

LIST OF FIGURES

1 INTRODUCTION

Movement is a characteristic fundamental to all organismal life. From wind-dispersed plant seeds to trans-continental migratory birds, movement provides a mechanism by which organisms can successfully seek out favourable habitats necessary for survival and reproduction. Evidence of our fascination with and desire to understand movement, particularly in animals, dates back to the 4th century B.C., when philosophers such as Aristotle acknowledged the astounding variety of movement abilities and posed the challenge of understanding the basic principles underlying the origins and consequences of movement. In taking up this challenge, movement research has considered a variety of scales and processes, from the biomechanics of bacteria movement (Berg 2000, McBride 2001) to the longest mammalian migration in humpback whales (Rasmussen et al. 2007). Indeed, animal movement is a phenomenon that encompasses multiple spatial and temporal scales, and has consequences for the structuring of individuals, populations, communities and ultimately ecosystems (Turchin 1998, Hanski 1999, Nathan et al. 2008).

In the past, it has been commonplace to study the components of movement processes in isolation; recently, however, a unifying conceptual framework has been proposed that integrates all facets of movement research into a paradigm that seeks to provide mechanistic generalities of movement behaviour across multiple scales and taxa (Nathan et al. 2008). This framework, developed by Nathan et al. (2008), has been termed the "movement ecology paradigm". It is made up of three basic components related to an individual organism (internal state, motion capacity and navigation capacity) and a fourth component related to external factors (biotic and abiotic) affecting its movement path (Fig. 1.1). It is important to recognise the presence of dynamic interactions between these components, which combine to influence a realised movement of an animal. The development of tracking technology has precipitated the development of the framework, which has shifted the focus from observing movements of animal populations to quantifying the movement of individuals (Nathan et al. 2008).

The movement ecology framework is primarily focused on the causes and consequences of movement of individuals. This approach provides an important perspective,

however, it fails to address how movement choices of individuals relate to, and impact on, community level processes. In this thesis, I combined the framework of Nathan et al. (2008) and ideas from community ecology to develop a multi-level approach to the study of the movement ecology of Afrotropical waterbirds. By adopting this integrated approach I aimed to provide a holistic understanding of waterbird movements.

1.1 Movement strategies

A vast amount of research has been devoted to understanding a particular mode of movement in animals - that of migration (Baker 1978, Swingland and Greenwood 1983, Holyoak et al. 2008). Long distance bird migration in particular has been extensively studied (Gauthreaux Jr 1982, Berthold 2001, Newton 2008, Rappole 2013). Migration in birds can be broadly defined as a series of predictable and regular movements between two locations in response to changes in local environmental conditions (Rappole 2013). Movements usually happen annually on a seasonal time scale, where birds move from their breeding grounds in summer to non-breeding grounds in winter. Movement in this sense is an adaptation that allows birds to exploit different environments for breeding and survival (Berthold 2001). A typical example of this behaviour is illustrated by Palearctic shorebirds which breed in the high northern latitudes of Eurasia, and migrate via flyways to sub-Saharan Africa in the austral summer (Hockey and Douie 1995). In this instance, departure from the breeding grounds is a response to changes in environmental conditions and can be triggered by cues such as changes in photoperiod (Berthold 1996) and weather patterns (Ramenofsky and Wingfield 2007).

There are, however, a myriad of other movement patterns such as local seasonal movements, partial migration, and nomadism (Rappole 2013), which are less well understood. It is important to note that avian movements fall within a continuum bounded by long-distance migration and resident behaviour on each extreme. When attempting to assign a particular movement pattern to a particular species, an additional level of complexity arises when different populations of that species exhibit contrasting movement patterns. A well-documented example of this is partial migration in Blue Tits *Cyanistes caeruleus*, where migrant and resident populations of a species breed sympatrically, but spend the non-breeding winter apart (Nilsson et al. 2010, Chapman et al. 2011). The nomadic movement mode of birds is particularly relevant to my study, and a considerable portion of this thesis

aimed to further our understanding of the causes and consequences of nomadism in southern African waterbirds. More specifically, I aimed to understand the role of environmental landscape characteristics as drivers of this aseasonal movement.

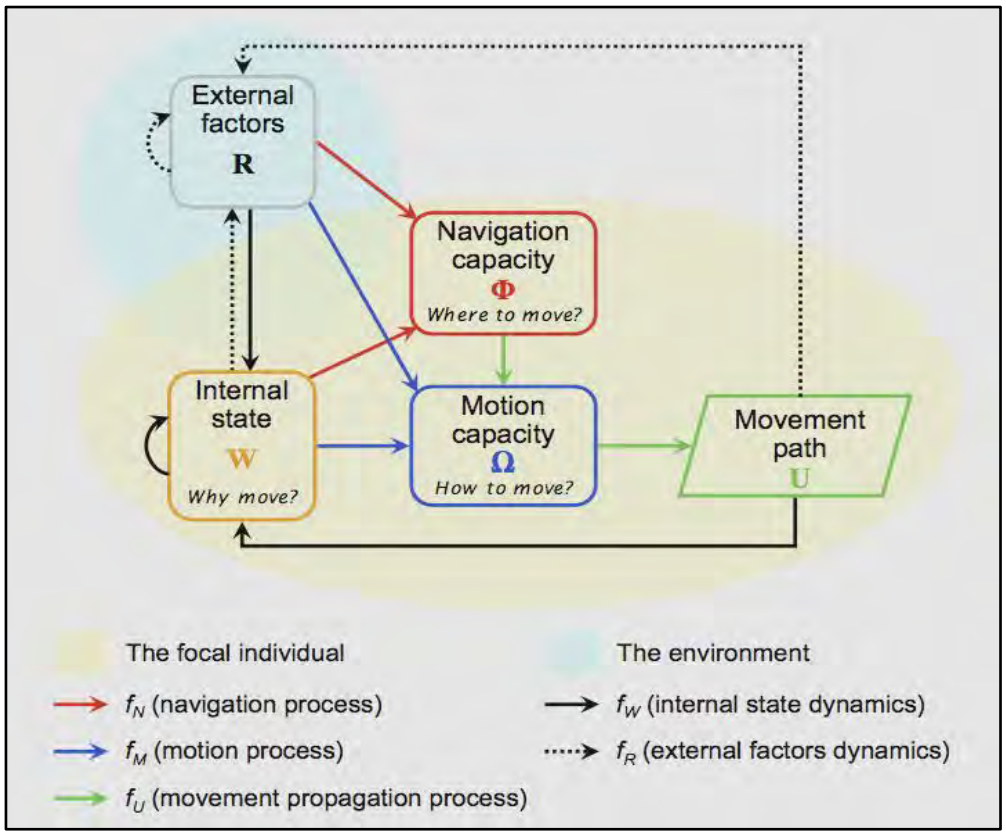


Figure 1.1 The conceptual movement ecology framework proposed by Nathan et al. (2008). The framework describes how the measureable realised movement path of an individual (U) is a result of the interaction between internal and external components. The internal state of the individual (W), the traits which enable movement (Ω), the ability to orient in space (Φ) as well as how these three components are affected by environmental factors (R), combine and interact to produce U. The yellow shading encompasses movement components that relate to the individual, while the blue shading corresponds to external abiotic and biotic factors. Lines joining the components represent inter-relationships, while the arrows indicate the direction of the effect.

1.2 Nomadism

Nomadism can be thought of as a set of seemingly unpredictable movements, which fall on the spectrum between migratory and sedentary movement patterns. The primary driver of nomadism is the relatively high level of spatiotemporal variability in environmental conditions within a species' range (Dean 2004). This results in population patterns which vary greatly over broad spatial extents and show a lack of annual consistency (Mueller and Fagan 2008a). In waterbirds, this movement pattern is most commonly observed in arid southern hemisphere landscapes (Roshier et al. 2001, Dean 2004, Dean et al. 2009). Rainfall in these landscapes is one of the primary limiting factors of wetland habitat availability, and its relative unpredictability in both magnitude and timing results in highly dynamic resource distributions (Jonzén et al. 2011).

As the majority of waterbird research has been conducted in temperate northern hemisphere systems (Baldassarre and Bolen 2006), we have a poor understanding of the proximate drivers of waterbird movement in arid landscapes. Understanding movements in a nomadic context in southern Africa has focused primarily around passerine birds (Dean 2004, Dean et al. 2009), while only a handful of studies have addressed nomadism in waterbirds (Cumming et al. 2012a, Ndlovu et al. 2013). Waterbirds in southern Africa therefore provide an ideal case study in which to further our understanding of movements of animals which are not under the influence of predictable and highly seasonal environments.

1.3 Waterbirds and wetlands

Research into wetlands and their associated fauna and flora is especially relevant in this day and age, as these ecosystems are facing significant threats to natural functioning from habitat loss and degradation, invasive species, pollution and climate change (Allan and Flecker 1993, Dudgeon et al. 2006, Kingsford 2011). Waterbirds form an integral part of wetland trophic systems and are entirely dependent on them for breeding, feeding, moulting, and ultimately their survival. Waterbirds provide a multitude of ecosystem services including provisioning (e.g. protein), supporting (e.g. propagule dispersal and nutrient cycling), regulating (e.g. pest control) and cultural services (Green and Elmberg 2014). One of the roles they play in terms

of supporting services is that of bioindicators of fish, invertebrates, macrophytes and water quality (Amat and Green 2010). Highly mobile species, in which populations show high spatial and temporal variation, can be hard to effectively monitor (Thomas et al. 2015). The effectiveness of using waterbirds as indicators of ecosystem change therefore rests on our ability to elucidate the mechanisms driving wetland use by waterbirds. Insight into waterbird movement ecology thus has the potential to play an important role contributing to the assessment of ecological health in wetland ecosystems.

In this thesis I follow the definition of waterbirds as species which are ecologically dependent on wetlands for breeding and survival, but exclude pelagic seabirds (Wetlands International 2012). Southern Africa has a diverse waterbird fauna; the individual-level analyses considered two species from the Anatidae family, while the community-level analyses considered 53 species from 15 families (Table 1.1).

Table 1.1 The analyses in this study considered southern African waterbird species from 15 families.

Family	Taxa
Anatidae	Ducks and Geese
Anhingidae	Darters
Ardeidae	Herons and Egrets
Burhinidae	Thick-knees
Charadriidae	Plovers
Jacanidae	Jacanas
Laridae	Gulls and Terns
Pelecanidae	Pelicans
Phalacrocoracidae	Cormorants
Phoenicopteridae	Flamingos
Podicipedidae	Grebes
Rallidae	Rails and Crakes
Recurvirostridae	Stilts and Avocets
Scolopacidae	Sandpipers
Threskiornithidae	Ibises and Spoonbills

In southern Africa there is documented evidence of wetland loss, particularly in the eastern half of region, where agricultural practices and human expansion have led to a decrease in the extent of floodplains, rivers, marshes and well-vegetated wetlands (Cowan 1995). Concomitant with this loss are range contractions and population decreases of several southern African waterbird species (Okes et al. 2008). This is of particular concern given that southern Africa is a generally water-scarce region.

Semi-arid conditions are common over most of southern Africa, where the regional mean annual precipitation is 475mm. There is a noticeable increasing rainfall gradient from western (~60 mm) to eastern parts (~800 mm) of the region (Tyson and Preston-Whyte 2000). The majority of precipitation occurs in the summer months from September to March. Drought periods are common and can often last several years. Rainfall is often in the form of short, heavy thunder showers which can be localised and highly variable in magnitude. Compared to northern latitudes, southern Africa is relatively depauperate in the abundance of natural wetlands. Much of the natural wetland habitat used by waterbirds is in the form of pans or vleis, which are ephemeral rain-fed shallow depressions.

The recent expansion of agricultural practices into the more arid regions has, however, brought with it an increase in the abundance of impoundments, used primarily for irrigation storage and stock watering. These farm dams have become important feeding and breeding refugia for waterbirds (Petrie and Rogers 1997a, Froneman et al. 2001, Raeside et al. 2007, van Niekerk 2010), and have contributed to the westward expansion of several species (e.g. Black-winged Stilt *Himantopus himantopus* and Blacksmith Lapwing *Vanellus armatus* (Okes et al. 2008)).

1.4 Southern African movement research

To review the recent approaches to understanding waterbird movements in southern Africa, I will refer to three primary sources of data: ringing recoveries, waterbird surveys and telemetry studies. Ringing of birds in the region dates back to as early as 1948, and is currently administered by the South African Bird Ringing Unit (SAFRING). Since the inception of SAFRING, over one million birds from 810 species have been ringed (Underhill et al. 1991). Within non-marine waterbirds, the majority of effort has centred on species within the Anatidae and Scolopacidae families (Oatley and Prys-Jones 1986, Underhill et al. 1999). For example, 26 239 Curlew Sandpipers *Calidris ferruninea* were ringed between

1972 and 1980, while up until 1999 there were four species of anatids that contributed 88 206 ringed individuals (Egyptian Goose *Alopochen aegyptiaca* 7 008, South African Shelduck *Tadorna cana* 9 507, Yellow-billed Duck *Anas undulata* 58 543 and Red-Billed Teal *Anas erythrorhyncha* 13 148).

While there has been considerable ringing effort, in most cases the number of recoveries has averaged 1.05% (Underhill et al. 1991). Although this figure may seem very low, those ringed birds that have been recovered have still provided valuable insights of movement patterns of waterbirds. For instance, the extent of movement and migration of southern African ducks was previously unknown, but ringing recoveries of Knob-billed Duck *Sarkidiornis melanotos* suggested that this species performs intra-African migrations (Oatley and Prys-Jones 1986), and is possibly the only southern African anatid to do so (Hockey et al. 2005). Knob-billed Ducks have been recorded to have moved a maximum distance of 3 879 km from a ringing site Zimbabwe to north of the equator into Chad (Fig. 1.2). The birds in Zimbabwe are thought to have been ringed during their overwintering period, after having moved from the breeding grounds in north-central Africa (Underhill et al. 1999). These movements are thought to be in response to rainfall and wetland availability, with birds moving away from shallow ephemeral breeding wetlands at the end of the wet season to more permanent wetlands in the winter period. Furthermore, data from ringing recoveries have given us an idea of the multitude of directions and distances that individual birds disperse, as well as providing information on important wetlands that waterbirds use.

Insight from ringing recovery data also allowed ornithologists to begin forming a general picture of the nature of species movement, with different waterbird movements being described as “relatively restricted dispersers”, “nomads” and “partial migrants” (Oatley and Prys-Jones 1986), as well as dispelling long-held beliefs (e.g. Curry-Lindahl (1981) held strong opinions that Yellow-billed Ducks were highly migratory, but results from ringing recoveries did not provide any substantive evidence for this). For certain waterbirds, such as Curlew Sandpiper, spatial information in the form of migration routes and distances have made a significant contribution to the understanding of this species’ ecology (Elliott et al. 1976).

There are, however, several limitations to using ringing recovery data. For instance, because of the low recovery rate it is difficult to understand the roles that factors such as age, gender, landscape, and climatic variation, have on observed movement patterns. There is also inherent bias in geographical location, as illustrated in ringing data from southern African

ducks, in which the majority of birds were ringed at a single site (Barberspan Nature Reserve, North West province, South Africa). In addition, ringing efforts have decreased substantially in the last two decades, with no major ringing programmes currently in place. This means that the utility of ringing recovery data of waterbirds is likely to decrease in the future.

Waterbird census projects, in a number of forms, have been undertaken in many important wetlands around the world for several decades (Wetlands International 2012). This is also the case for southern Africa where, in a number of wetlands, monthly waterbird counts have been carried out for the past 30 years (Kalejta-Summers et al. 2001a, 2001b). Waterbird population monitoring was formalised in 1991, following the inception of the Coordinated Waterbird Counts in South Africa (CWAC) programme. By the winter of 1997, surveys were being conducted at 154 wetlands across the country by a combination of conservation organisations and citizen scientists (Taylor et al. 1999). This number has increased to incorporate approximately 370 wetlands. At each wetland, counts are performed twice a year, once in midsummer (January) and midwinter (June).

The primary objectives of the CWAC project are to monitor population trends across as many wetlands as possible; to understand how species' abundances fluctuate through different seasons; to identify which species are distributed across different wetlands through space and time to detect movements; and to collect data to detect long-term population trends (Taylor et al. 1999). In a review of the data collected between 1992 and 1997, Taylor et al. (1999) found several notable site and species patterns. The project was able to identify the important wetlands which host significant populations of waterbirds in both a regional and global sense. This allowed for the identification of sites which met the criteria of Important Bird Areas (IBA, www.birdlife.org) and RAMSAR sites. Interestingly, 46% of the count sites were located in artificial habitats (e.g. agricultural dams, large reservoirs, salt works and waste-water treatment works), and the census results revealed how important these sites were, both from abundance and diversity perspectives. This was especially apparent for species from the Anhingidae and Ardeidae families (Taylor et al. 1999).

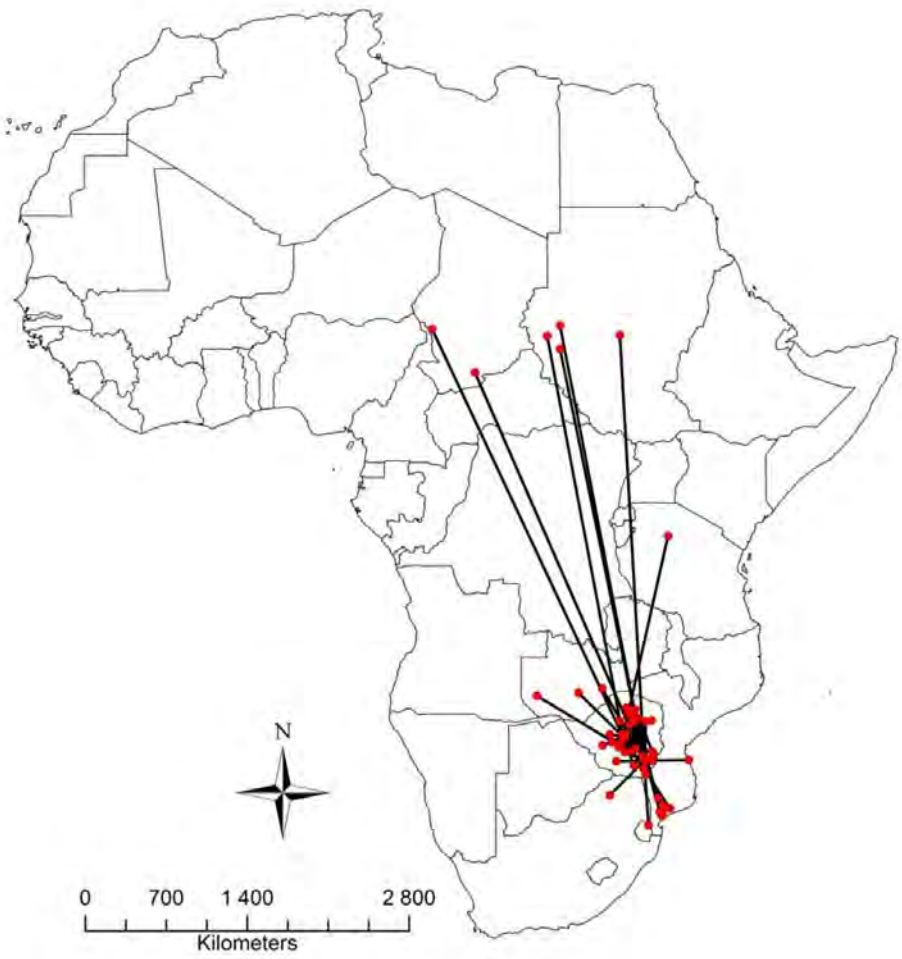


Figure 1.2 Movement of Knob-billed Ducks which were ringed between 1965-1979 in Kwekwe and Chiredzi, Zimbabwe. Black lines indicate great-circle distance between capture and ring recovery sites (red points).

In analysing the species data, the CWAC project revealed interesting patterns of waterbird movement at the population level. Some of the more general findings were that many populations showed marked fluctuations in abundance between seasons, with many species moving from inland sites to coastal areas in winter. There were also striking patterns of increased abundance of populations at permanent wetlands in winter compared to abundance in summmer, which provided new insights into species that were thought to be highly sedentary. This suggested that many waterbird species do exhibit nomadic behaviour by dispersing to ephemeral wetlands when water and food availability were high. The results

proved to be more useful at illuminating patterns of local waterbird movements across the region compared to those of inter-continental migrants. Since this review, census data have been used to illustrate how movements of different waterbird families into wetlands fluctuates throughout the years in response to rainfall (Harebottle et al. 2008) and how waterbirds respond to hydrological changes and habitat availability (Kalejta-Summers et al. 2001b, Whittington et al. 2013). Data have also been used for applied conservation questions, such as the formulation of a waterbird conservation value score, which measures the overall conservation importance of a specific wetland to waterbirds (Harebottle 2012).

There are, however, limitations of the census protocol for providing more detailed patterns of waterbird movement, such as the coarse temporal resolution of surveys, methodological bias resulting from the lack of standardisation of observers and survey routes, uneven distribution of count sites geographically and across different wetland types, and the inability to accurately survey the more cryptic species from families such as the Rallidae. The limitations of ringing recovery, waterbird surveys, and atlas data in detecting movement patterns of Red-billed Teal has been made clear by Thomas et al. (2015), who combined these three data sets to evaluate their performance at resolving movement in Red-billed Teal. Thomas et al. (2015) concluded that this inability to accurately detect movement patterns was the result of a failure to incorporate ideas of spatial and temporal variation into the monitoring protocols.

Telemetry data are the third source of data that has been used to understand waterbird movements, however the number of southern African studies is extremely low. Prior to my study there have only been two other telemetry-focussed studies (note that in making generalisations here about the various telemetry studies in the region, I do not include those of Cumming and Ndlovu (2011), Ndlovu (2012), Cumming et al. (2012), and Ndlovu et al. (2013), of which my data and analysis is part). Petrie and Rogers (1997b) managed to track two individual White-faced Ducks *Dendrocygna viduata* on the Nyl River floodplain, South Africa for a period of about 8 months. While this was an important first step to obtaining fine-scaled data quantifying the movement of waterbirds, the conclusions from the study were limited due to the low sample size, relatively short tracking duration and the fact that the birds did not move more than 85 km from the capture site. In an effort to investigate post-breeding dispersal patterns, McCulloch et al. (2003) tracked five Lesser Flamingos *Phoeniconaias minor* and three Greater Flamingos *Phoenicopterus ruber roseus* captured in the Makgadikgadi salt pans of Botswana. The results illustrated the nomadic behaviour of

flamingos as well as the importance of small wetlands as important non-breeding sites. There have been, however, a number of waterbird tracking studies in other regions of sub-Saharan Africa. Seven Lesser Flamingos were captured in Lake Bogoria in central Kenya, and were tracked between 2002 and 2004 (Childress et al. 2004, 2007). Again, the data were used to illustrate the nomadic movement patterns of Flamingos and identify a key network of alkaline wetlands. Additionally, the connectivity of east African populations was assessed (Salewski et al. 2009). These were important findings, given the Near Threatened IUCN status of the Lesser Flamingo.

The second significant waterbird telemetry study focused on five species of Afrotropical waterfowl: Fulvous Duck *D. bicolor*, Garganey *Anas quequedula*, Knob-billed Duck, Spur-winged Goose *Plectropterus gambensis* and White-faced Duck (Gaidet et al. 2010, Cappelle et al. 2011a, 2011b, Takekawa et al. 2015). The study mentioned above was more geographically extensive with higher sample sizes than previous studies; between 2-21 individuals of each species were tagged in Mali, Nigeria and Malawi. The data were primarily used in an epidemiological context to understand the potential role of waterbirds as vectors of avian influenza viruses (AIVs, Gaidet et al. (2010)) and quantify risk of disease transmission between wild and domestic bird populations (Cappelle et al. 2011a). In a review of the movements of the tagged birds, Takekawa et al. (2015) summarised parameters of movement for each individual (e.g. daily distance moved, direction, movement rate). In all of the studies mentioned above on flamingos and ducks, only Cappelle et al. (2011a) took the analysis further than merely summarising descriptive movement parameters and mapping out movement paths; Cappelle et al. (2011a) combined remote sensing and telemetry data to construct predictive movement models.

Common threads among all the other studies are that they lacked a theoretical context for analysing movements, they did not analyse the data within a movement modelling framework, and they did not quantify landscape characteristics by making use of remotely sensed data. The outcome is that conclusions which can be drawn about the mechanisms and processes driving waterbird movement are severely limited. There have been several advances in tracking device technology and analytical techniques which mean that telemetry studies now have the ability to not only answer where waterbirds move, but also address important questions of how and why they do so.

1.5 Advances in movement research

Advances in telemetry technology mean that we can now track animals, some as small as insects (Kissling et al. 2014), with high spatial precision over broad geographic and temporal extents (Tomkiewicz et al. 2010, Kays et al. 2015). Remote observations of animal movements can now extend into previously inaccessible environments such as oceans and deserts (Boyd et al. 2004, Kooyman 2004). This coupled with the development of novel movement models and analytical techniques, means that we are now able to address a number of fundamental questions relating to habitat use, migration, behaviour and evolution of animals (Cagnacci et al. 2010). The vast quantity of accessible remotely sensed data has provided the opportunity to establish links between the movement path of an animal and the physical landscape characteristics across which it is moving. This framework provides a basis for revealing mechanisms driving a variety of fundamental ecological patterns, such as home range behaviour (Kie et al. 2010, Smouse et al. 2010), habitat selection and resource use (Beyer et al. 2010, Fieberg et al. 2010), functional responses (Mysterud and Ims 1998, Hebblewhite and Merrill 2009) and population dynamics (Morales et al. 2010). Advances in data storage and processing tools also mean that the opportunities to conduct these studies are now available to a wide array of researchers (Urbano et al. 2010).

Numerous statistical frameworks and movement models for analysing data now exist. These range notably in their complexity (Schick et al. 2008). There are methods such as fractal analysis (Nams and Bourgeois 2004, Roshier et al. 2008b), random walks (Turchin 1998) and Lévy movements (Viswanathan et al. 1996), which focus on using descriptive parameters of movement paths such as turning angles, net squared displacement and step lengths. More recent methods include first-passage time analysis (Fauchald and Tveraa 2003, 2006), residence time analysis (Barraquand and Benhamou 2008) and state-space models (Jonsen et al. 2005, Patterson et al. 2008), which seek to identify changes in behavioural states of a focal individuals based on combining theoretical assumptions of behavioural change with the statistical properties of different movement modes.

1.6 Study aims

The design of this thesis was motivated by three primary factors: (1) the movements of waterbirds occupying semi-arid landscape are poorly understood, given that the majority of our understanding originates from northern hemisphere studies, where the spatial and temporal distribution of landscape resources are largely predictable; (2) the studies that have used census and telemetry data in the region have been unable to provide a mechanistic understanding of waterbird movements; and (3) there is a lack of multi-scale studies which combine the analysis of movements of individuals and the high spatial and temporal variance in species abundances that are seen in waterbird communities.

In this study I aimed to bridge these gaps by analysing fine-scale telemetry data of two species of Afrotropical waterfowl (Egyptian Geese and Red-billed Teal) within the framework of established theoretical movement models. By analysing waterbird census data, I then aimed to use movement as a basis for testing ecological theories related to the structure and persistence of waterbird communities. In doing so, I provided an integrated approach to addressing questions of waterbird movement in arid environments. This work builds on that of Ndlovu (2012) and Cumming et al. (2012a), who have provided a solid basis for further exploring movements of waterbirds in dynamic landscapes. In exploring movements of waterbirds I aimed to go beyond the "where" to address the "how" and "why".

1.7 Thesis outline

Each chapter is structured and presented as a stand-alone paper to facilitate publication. This has resulted in repetition of certain themes in the introduction sections, although efforts have been made to keep this to a minimum. In Chapter 2, which is not intended to be a publishable paper itself but provides much of the background for the other chapters, I provide an overview of the study sites and field methods that were used to generate the data for the four individual chapter analyses. First, I describe the details of telemetry data from Egyptian Geese and Red-billed Teal, including how the birds were tagged, where they were tagged and the number of individuals used in the analyses of Chapters 3 and 4. I then introduce the data used in Chapters 5 and 6, which are a combination of waterbird count and environmental data collected at 60 wetland sites in KwaZulu-Natal, South Africa. I provide a description of the landscape and sites in which the study took place. Following that I describe the protocol for

collecting the various components of data as well as providing a summary of environmental measurements across my study sites. I have devoted two chapters to each aspect of my integrated approach. Chapters 3 and 4 are based on movement data from individual waterbirds and Chapters 5 and 6 are based on waterbird community count data collected across a large network of wetlands over a 14 month period.

Understanding which resources are selected more often than others provides essential insight into how animals meet their requirements for breeding and survival. Resource-selection functions (RSFs) can be used to answer a number of questions related to habitat selection. For instance, what resources are limiting to an animal and how do patterns of habitat use vary through life stages and across landscapes? Waterbirds are highly mobile which allows them to potentially alter their habitat use over short temporal scales. In Chapter 3, I address two primary questions: (1) is habitat selection of Egyptian Geese at the home range scale influenced by variation in life stage (i.e. internal factors) or by season and sites (i.e. external factors); and (2) do Egyptian Geese prioritise habitats that provide high quality forage or those which minimise the risk of predation? For the former, I use point-based telemetry data from two Egyptian Geese populations and analyse it within a RSF modelling framework. I use GIS land cover data to define five discrete habitat categories. To answer that latter question, I use a functional response framework for investigating the forage-predation trade-off.

By linking movement paths with landscape conditions it is possible to detect the important environmental drivers of movement behaviour across broad spatiotemporal gradients. In Chapter 4, I extend my analysis beyond movements which are quantified by point-based telemetry data to those which are quantified by trajectory-based data. Additionally, instead of defining discrete habitat categories, I use dynamic landscape variables to quantify environmental conditions. The properties of an animal's trajectory, such as speed and frequency of turns, can be used to infer the profitability of a habitat patch. Animals should move slowly and tortuously through habitats that positively affect their fitness - behaviour that is termed Area-Restricted Search (ARS). Identifying these profitable areas is a fundamental step in understanding how animals adjust their movements in response to landscape dynamics. In Chapter 4 I use a first-passage time movement model with trajectory-based telemetry data from Egyptian Geese and Red-billed Teal to test whether birds display ARS behaviour, and if so, what are the important environmental conditions associated with this behaviour. I also test two competing movement hypotheses: whether

movements of waterbirds are prescient or reactive in response to the dynamics of landscape variables.

Ecological communities are often characterised by species which possess varying degrees of movement ability. This in turn has consequences for community structure and composition which can be affected by behaviours such as inter-specific competition between migrant and resident species. Understanding the ecological niches of interacting species can provide insight into how movement shapes the life history and ecological traits of a species. I use waterbird count data in Chapter 5 as a community-level approach to assess the relative ecological niches of waterbirds with different movement, dietary and foraging habitat functional traits. I address two primary questions: (1) do waterbirds with greater movement ability respond to broad scale environmental variation; and (2) do specific environmental variables filter waterbird functional traits? I analyse the community count data within a functional trait framework and use novel multivariate techniques to reveal environmental-trait associations.

Dispersal plays a fundamental role in linking assemblages within metacommunities (i.e. a set of local communities). Disentangling the role of spatial (i.e. dispersal) and environmental factors provides important insight into the multi-scale processes operating on and structuring metacommunities. An aspect that has rarely been considered is how these processes vary in importance through time. In Chapter 6, I use the metacommunity framework to test the relative influences of spatial and environmental factors driving waterbird community structure over a 14 month period in a network of wetlands in KwaZulu-Natal, South Africa. I explore the importance of movement, in the form of dispersal between sites, in determining community patterns. In addition, I test the effect of temporal variation and whether community processes change through sampling periods. I use a variance partitioning approach to analyse the data and discriminate between four community assembly mechanisms; species sorting, patch dynamics, neutral models and mass effects.

In the final chapter I summarise my findings and present a general discussion of theoretical insights gained from integrating individual and community-level movement perspectives. I also show the contribution that this work makes to understanding, in a more general sense, the movement ecology of waterbirds in a highly dynamic semi-arid environment.

2 GENERAL METHODS AND STUDY SITES

2.1 Sites and telemetry data

I used telemetry data from two species of southern African waterfowl, Egyptian Goose and Red-billed Teal, in Chapters 3 and 4. The precise data analysed in each chapter did, however, differ in the number of individuals used and the origin of the tagged individuals (Table 2.1). Egyptian Geese and Red-billed Teal were tagged with satellite GPS platform transmitter terminals (30 and 22g PTTs respectively; Microwave Telemetry Inc., Columbia, MD, USA). PTTs were attached to the birds using a teflon ribbon backpack harness. Waterfowl were captured using mist nets and maize-baited walk-in traps (Cumming et al. 2011). PTTs were set to record a GPS location every 2 h for geese and 4 h for teal, and data were transmitted to the Argos satellite every three days; for details of transmitter attachment methods and success rates, see Cumming and Ndlovu (2011). Birds were tagged immediately after they had completed moult, which allowed us to confirm the wetlands as moulting sites. The individually tracked waterfowl chosen for this study were a subset of a larger group of geese and teal tagged at the respective study sites (Cumming and Ndlovu 2011). In Chapter 3, I only used data from Egyptian Geese that were tracked for a minimum of 11 months, while in Chapter 4, geese and teal tracked for less than 90 days were excluded from the analysis.

Table 2.1 Number, species and tagging site of individuals from which telemetry data were used for each chapter. STR, Strandfontein; BAR, Barberspan; MAN, Lake Manyame, JOZ, Jozini Dam.

	Species	STR	BAR	MAN	JOZ	Total
Chapter 3	Egyptian Goose	4	6	-	-	10
Chapter 4	Egyptian Goose	7	6	2	4	19
	Red-billed Teal	5	4	5	-	14

The birds in my study population were captured at three wetland sites in South Africa and one in Zimbabwe: Strandfontein wastewater treatment works; Barberspan Nature Reserve; Jozini Dam and Lake Manyame, respectively (Fig. 2.1 and Table 2.1). Strandfontein experiences a Mediterranean climate with wet winters and hot dry summers. In contrast, Barberspan, Lake Manyame and Jozini Dam fall within a summer rainfall region with hot, wet summers and mild dry winters. For a detailed description of each site see Cumming et al. (2011). Semi-arid conditions are common over most of southern Africa; mean rainfall over the entire region is 475mm. There is a gradient of increasing rainfall moving from the western to eastern regions of the country (Fig. 2.2).

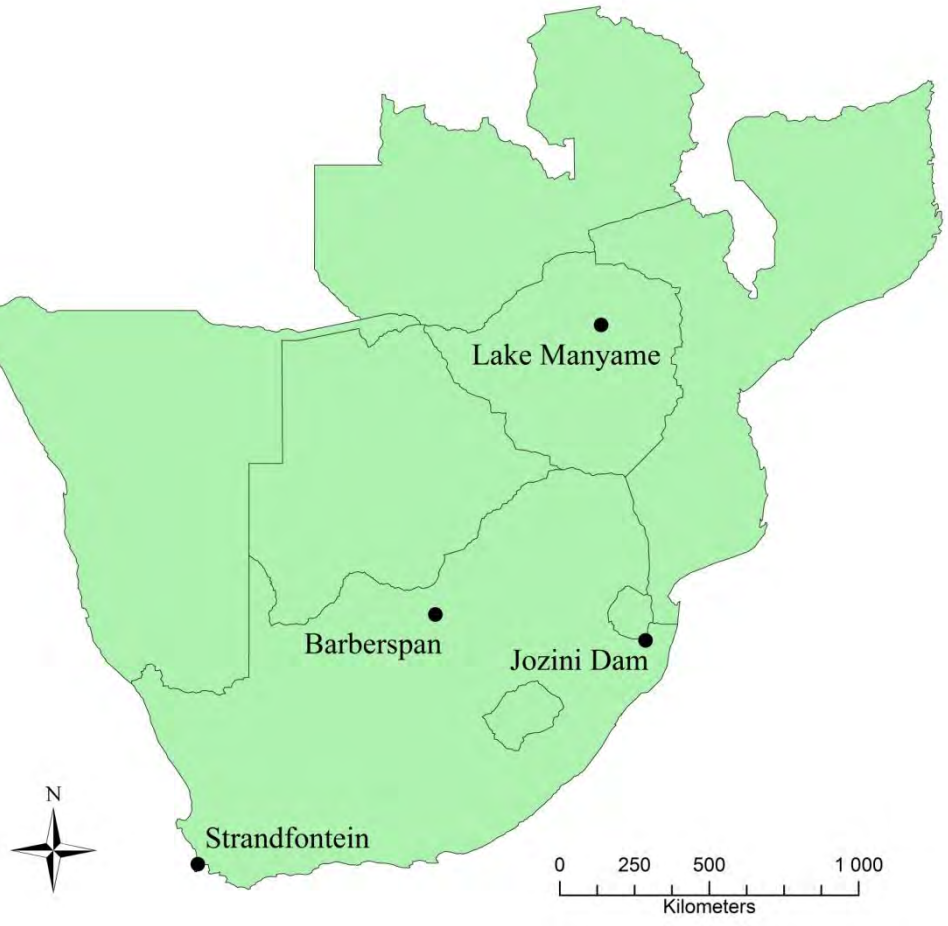


Figure 2.1 Location of the southern African capture sites at which Egyptian Geese and Red-billed Teal were tagged.

Table 2.2 Details of sites at which Egyptian Geese and Red-billed Teal were caught and tagged with platform transmitter terminals (PTTs).

	Rainfall ($mm.yr^{-1}$)	**Vegetation**	**Wetland type**	**Approx. size (ha)**	**GPS coordinates**
Barberspan	553	Grassland	Natural pan	2 400	26°33' S, 25°37' E
Strandfontein	557	Fynbos	Sewage treatment	319	34°05' S, 18°20' E
Lake Manyame	805	Mixed savanna	Impoundment	18 500	17°49' S, 30°36' E
Jozini Dam	664	Coastal plain	Impoundment	13 200	27°20' S, 31°54' E

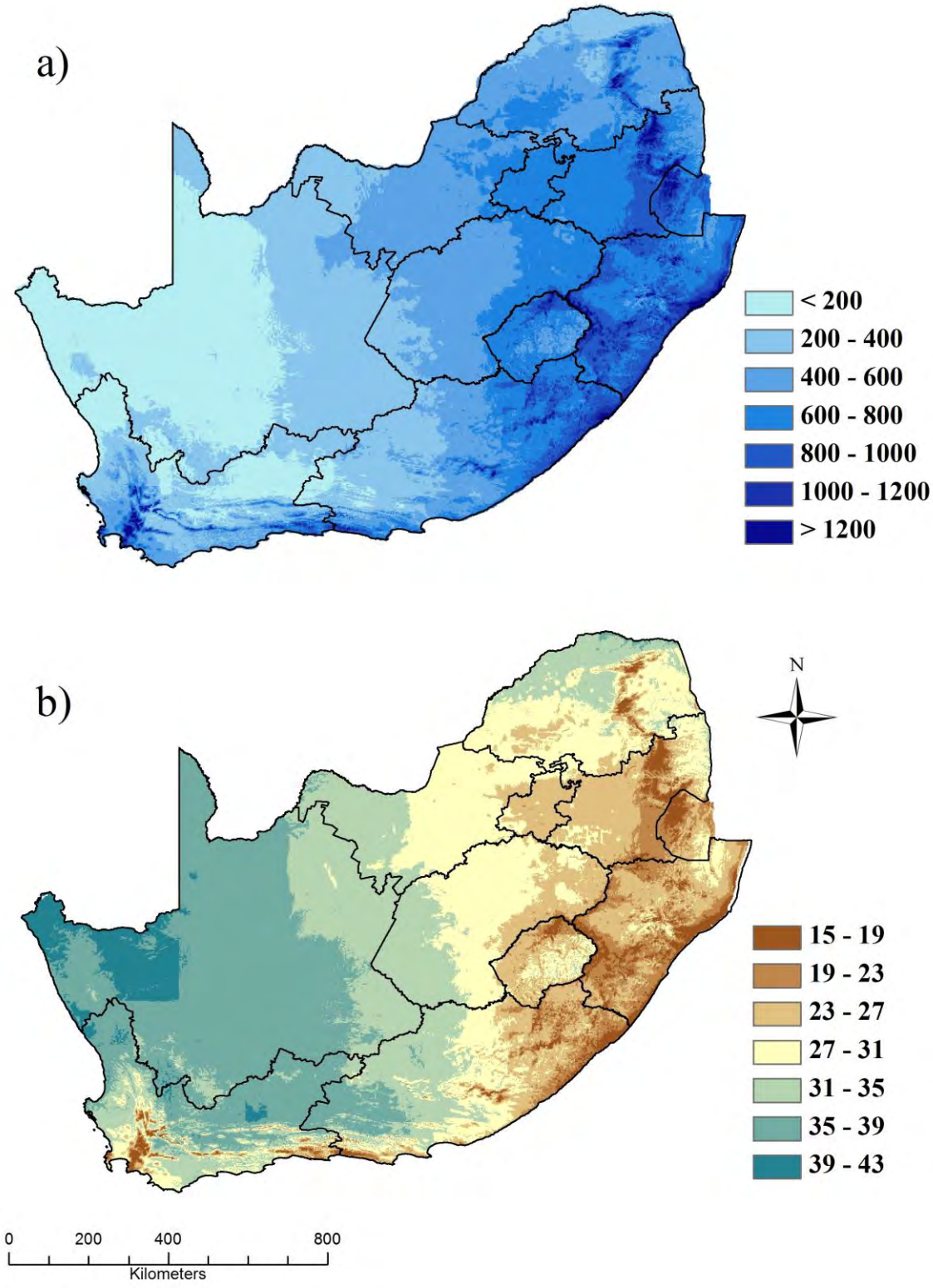


Figure 2.2 (a) Mean annual precipitation across South Africa illustrating an increasing gradient from west to east; (b) coefficient of variation of precipitation. Rainfall measured in mm and data sourced from Schulze et al. (2006).

2.2 Community and environmental data

In Chapters 5 and 6 I used waterbird community abundance data, collected from 60 wetland sites in KwaZulu-Natal, South Africa. Each site was characterised by four sets of environmental variables: vegetation structure, water quality, rainfall and land cover. I measured vegetation structure and water quality at each site during each sampling period. Land cover around sampling sites was derived from a GIS data set. Rainfall for each sampling period was measured using weather stations surrounding the sites. Sampling of both waterfowl abundance and environmental measurements was carried out from April 2012 to June 2013 with each site being sampled every second month, resulting in a total of eight repetitions per site.

The study was undertaken in the northern coastal plain of KwaZulu-Natal province. The plain extends 170 km from the town of St Lucia in the south to the Mozambique border in the north. The western and eastern boundaries were defined by the Lebombo Mountain range and the Indian Ocean respectively, a distance of approximately 75km. The study area is roughly 9 900 km^2 and falls within the Maputaland centre of endemism, which is characterised by high floral and faunal diversity. The climate is subtropical with wet, hot summers and mild winters. Annual rainfall, which is highly variable, ranges from 600 mm in the west to 1000 mm in the east and falls primarily in the summer months.

Accessible sampling sites were chosen to maximise coverage over a diversity of wetlands; the 60 point locations incorporated 14 different wetland systems (Fig. 2.3). Wetlands covered a wide range of hydrology, chemistry and vegetation types including estuarine systems, fresh water endorheic lakes, a large man-made dam, floodplains and swamps, and nutrient-rich pans. Many of the wetlands fall within nationally and provincially protected conservation areas, although the level of protection varies (notably, in certain wetlands protection only extends up to the high water mark, which allows people access to shoreline vegetation resources). Several wetlands are RAMSAR and Important Bird Area (IBA) sites.

Count sites were grouped into the following nine clusters (Fig 2.3) on the basis of proximity and habitat similarity: (1) False Bay in Lake St Lucia (FB); (2) eastern shores of Lake St Lucia (ES); (3) western shores of Lake St Lucia (WS); (4) Pongola floodplains (PF);

(5) Jozini Dam (JZ, also known as Pongolapoort Dam); (6) Lake Sibaya (SB); (7) Mtubatuba (MT); (8) Muzi pans (MZ); and (9) Kosi Bay lakes (KB).

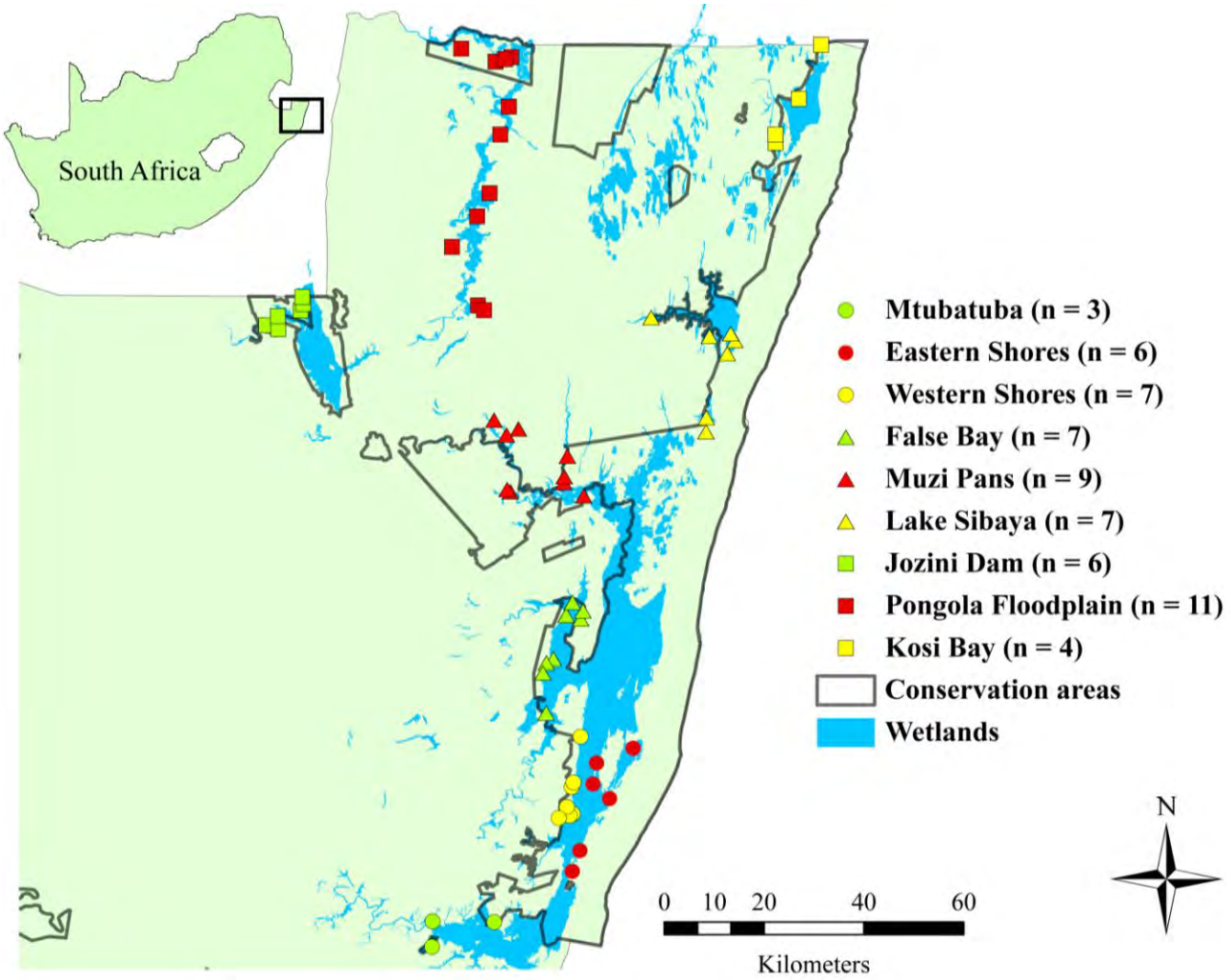


Figure 2.3 Map of 60 wetland sampling sites grouped by wetland cluster on the coastal plain of northern KwaZulu-Natal, South Africa.

Lake St Lucia, which is located within the iSimangaliso Wetland Park (a UNESCO World Heritage Site), is a large estuarine system made up of a series of interconnected lakes which drain into the Indian Ocean. Over the decades, the lake has experienced several extreme dry down periods in which maximum depth decreases to 3.5m and water chemistry ranges from fresh to hypersaline (Carrasco and Perissinotto 2010, Perissinotto et al. 2010).

Six and seven sites were sampled on the eastern and western shores respectively. Vegetation at sampling sites ranged from open exposed mudflats to heavily reeded shorelines.

Sites in the Pongola floodplain system include four semi-permanent pans within Ndumo Game Reserve and seven in rural areas along the course of the Pongola River. Water levels at these sites fluctuate with natural rainfall cycles as well as controlled discharge from the upstream Jozini Dam. Heavily wooded vegetation surrounds the pans in Ndumo, while wetlands along the floodplain are surrounded by rural settlements. The natural resources associated with the pans are heavily exploited by local communities through fishing, stock watering and reed harvesting. Pans are shallow and characterised by high proportions of emergent, reed bed and macrophyte vegetation.

The Jozini Dam, with a surface area of 132 km^2, was completed in 1974 with the aim of providing irrigation to surrounding agricultural areas. Sampling sites were located on the western shore of the dam within the Pongola Nature Reserve. Vegetation surrounding the dam ranges from grassland to Acacia thornveld. Water levels during the study were variable resulting in the presence of large sections of exposed mudflats in the drier months.

Lake Sibaya is South Africa's largest freshwater endorheic lake and has a surface area of 70km^2. The eastern shoreline of the lake is flanked by thick coastal dune forest, while patches of grassland surround the remaining shoreline areas. Four sites were located on the south eastern shores of the main body of the lake, and one site was located at a narrow inlet on the western side of the lake. The remaining two sites that make up this cluster were located in Sodwana Bay, to the south of Lake Sibaya. One of these sites was a small waste water treatment works and the other a small natural lake.

The Mtubatuba cluster is made up of two small dams and Lake Eteza, which is a shallow lake in a small nature reserve. The lake, which forms part of the Umfolozi river system, is surrounded by exotic tree plantations and sugarcane fields. Lake Eteza has very small areas of open water and much of the marginal vegetation is in the form of extensive reed beds. The two dams are located in close proximity to sugarcane farming operations and have extensive shrub and reed bed vegetation.

Sites in the Muzi pans cluster included two points on Nsumo Pan located within Mkhuze Game Reserve and the remaining sites along the floodplain of the Mkhuze River. These pans are shallow and water levels are linked to summer rainfall events. The floodplain

is set among a grassland-savanna vegetation matrix interspersed with patches of natural forest. As with the Pongola floodplain, use of wetland resources for subsistence by local communities is high.

The Kosi Bay wetlands, which lie just south of the Mozambique border, fall within an estuary-linked system comprised of four interconnected lakes. A salinity gradient exists from the mouth of the estuary and the water becomes fresher upstream. One sampling site was located with the Kosi bay Nature Reserve, while the other three sites were located at two small lakes bordering the reserve. The water in these wetlands is oligotrophic and clear, with low silt content and sandy substrates. Vegetation surrounding the wetlands ranges from thick coastal forests to grasslands interspersed with shrubby vegetation.

2.2.1 Sampling protocol

Waterbird counts

Standardised bimonthly point counts at 60 sites across the study area were carried out from April 2012 to June 2013. This resulted in 8 sampling replicates for each of the 60 sites. All counts were carried out within the first 10 days of each sampling month. Sites were sampled in the same order throughout the majority of sampling periods. Counts were conducted during one of four time periods (06h00 – 09h00, 09h00 – 12h00, 12h00 – 15h00, 15h00 -18h00). In order to avoid bias introduced by the time of day, each site was counted in the same time period throughout the sampling period. Counting commenced after a 10 min habituation period following arrival at a site to minimise the effect of observer disturbance. Counts lasted 30 min and all birds were counted within a semi-circle along the shoreline of 150 m radius. The 150 m distance was measured using a laser range-finder and landmarks in and near the water. All birds were assigned to a category of either foraging, non-foraging (e.g. roosting) and flying over. Birds recorded as flying over the count site were excluded from further analysis. All counts were carried out by the same two individuals (myself and David Nkosi, a highly experienced observer).

Vegetation sampling

Vegetation structure was assessed within the count area after bird counts were completed and comprised of two components: aquatic and shoreline. Vegetation structure differed markedly across my sample sites and Figure 2.4 illustrates the extremes of well-vegetated shoreline (Fig 2.4a) versus open shoreline (Fig 2.4b), and well-vegetated water column (Fig 2.4c)

versus open water (Fig. 2.4d). Aquatic vegetation cover was visually estimated by dividing the count area into four equal areas and recording the proportion of different classes (to the closest 5%) of vegetation for each segment. Three aquatic vegetation (AQ) classes were defined: (1) aquatic reeds and sedges (AQ-RS); (2) flooded grass (AQ-FG); and (3) emergent vegetation (soft stemmed plants), submerged vegetation and floating vegetation (AQ-SF). Segments devoid of vegetation were designated as open water. The total of each of these classes summed to 100%. In a similar manner shoreline vegetation was visually estimated by dividing the 150 m shoreline into four segments and recording structure while walking the length of the transect. Proportion of vegetation was recorded within 5 m of the water's edge. Three shoreline vegetation (SL) categories were defined: (1) shoreline reeds and sedges (SL – RS); (2) shoreline grass and mudflats (SL – GM); and (3) trees and shrubs (SL – TS). Segments which contained only rocky structure were designated as open shoreline. See Table 2.3 for a summary of vegetation structure variables across clusters.

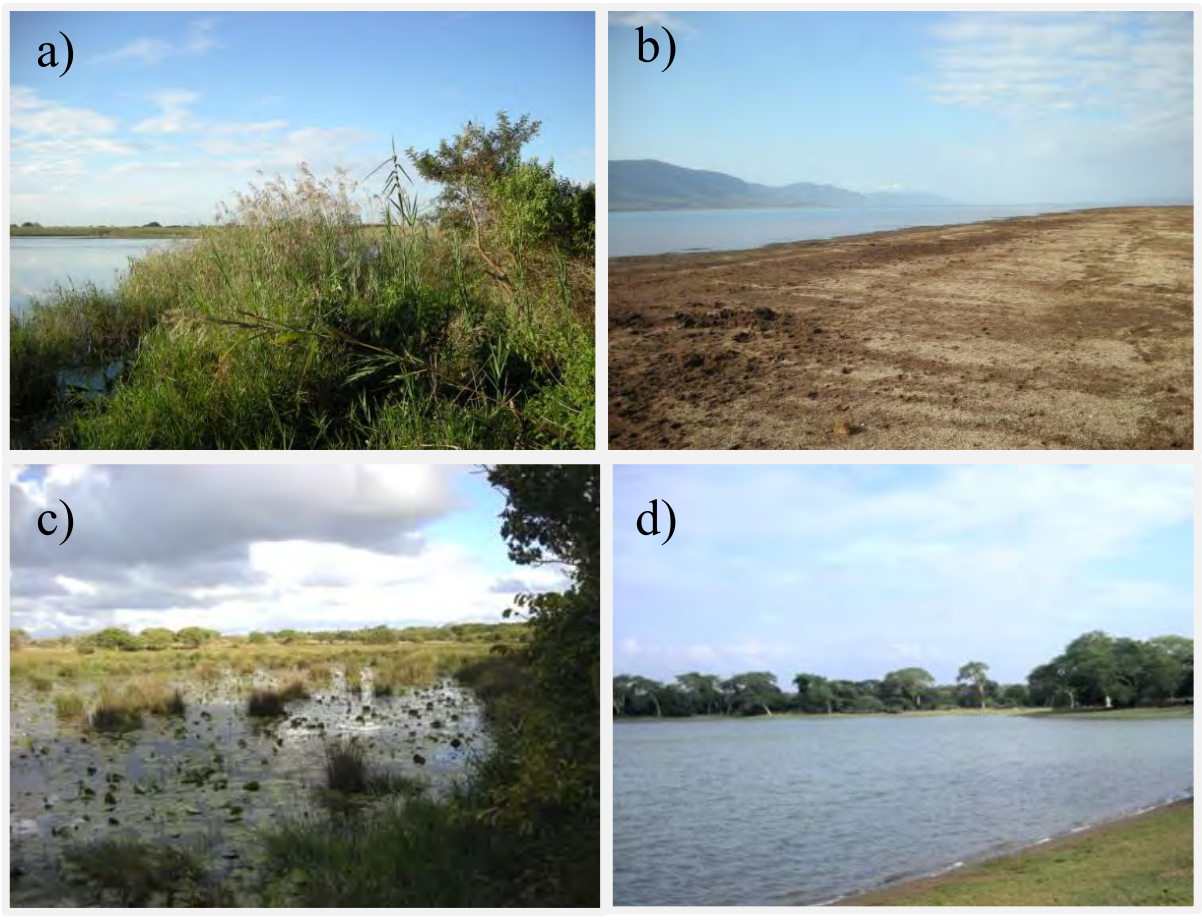


Figure 2.4 Photos of sites within the a) Mtubatuba cluster, b) Jozini Dam cluster, c) Eastern Shores cluster and d) Pongola floodplain cluster. Pictures illustrate the contrast of proportions of aquatic and shoreline vegetation between sites. Photographs: Dominic Henry.

Water quality measurements

Water quality measurements were taken at each count site throughout the study period using a HI9828 multi-parameter probe (Hanna Instruments, Cape Town, South Africa). The meter was calibrated before the start of each sampling period. It provided measures of pH (standard units), dissolved oxygen (DO, $mg.L^{-1}$), salinity (Sal, psu) and water temperature (Temp, °C). The probe was held about 10 cm under the surface and five readings from each site were taken. Values for water quality variables were subsequently averaged before inclusion into the analysis. See Table 2.4 for a summary of water quality variables for each cluster. Standard deviation measures in the Mtubatuba cluster were not calculated due to the absence of water quality measurement at two of the three sites. Water quality data were not available for the August 2012 sampling period. I therefore excluded all environmental and census data from August 2012 in the analyses of Chapter 5 & 6.

Rainfall

Three measures of monthly rainfall were used in this analysis. Rainfall variables were calculated as the total monthly rainfall in the preceding month (Rain 1), two (Rain 2), and three (Rain 3) months prior to the month in which bird counts were conducted (e.g. values for sampling in April 2012: Rain 1 = sum of rainfall in March 2012; Rain 2 = sum of rainfall in February 2012; Rain 3 = sum of rainfall in January 2012). Rainfall readings were obtained from measurement stations as close as possible to count sites. Rainfall data were provided by the South African Weather Service (SAWS, www.weathersa.co.za). In the case where SAWS stations were not in close proximity to a site, or where data were missing, data were provided by Ezemvelo-KZN Wildlife. See Table 2.5 for a summary of rainfall variables across sampling clusters.

Land cover

Land cover data were extracted from the 20 x 20 m resolution 2008 KwaZulu-Natal Land Cover dataset (Ezemvelo-KZN Wildlife 2011). The data were derived from SPOT5 multispectral imagery. A total of 1001 map accuracy reference points were used for ground-truthing, which resulted in 78.92% classification accuracy. Each pixel in the dataset corresponds to one of 47 classes. I combined the aggregated classes to form three groups of land cover: (1) rural, agriculture, degraded and anthropogenically modified (ANTHRO); (2) all natural vegetation (NATU); and (3) estuarine and freshwater wetlands (WET). The proportion of these land cover classes was measured within a 3 km buffer surrounding each

count site. Data were extracted and processed in ArcGIS version 10 (ESRI GIS software, Redlands, CA, USA, www.esri.com). See Table 2.6 for a summary across clusters.

Figure 2.5 Egyptian Goose attached with a GPS platform transmitter terminal. Photograph: Dominic Henry.

Table 2.3 Means and standard deviations of proportion of vegetation cover for each of the six classes grouped by site cluster and sampling period. Values are averaged across sites within each cluster. Number of sites in each cluster is given in parentheses. See text in *Vegetation sampling* and for explanation of vegetation structure codes.

Cluster	Sampling Period	SL-RS	SL-GM	SL-TS	AQ-RS	AQ-FG	AQ-SF
ES (n=6)	April 2012	14 ± 35	53 ± 40	16 ± 36	3 ± 6	13 ± 9	21 ± 35
	June 2012	2 ± 4	43 ± 37	18 ± 34	6 ± 16	12 ± 16	10 ± 24
	October 2012	7 ± 11	73 ± 34	19 ± 38	8 ± 12	4 ± 10	31 ± 40
	December 2012	22 ± 40	58 ± 48	20 ± 36	3 ± 6	33 ± 27	17 ± 32
	February 2013	17 ± 41	54 ± 40	24 ± 36	13 ± 14	16 ± 27	13 ± 33
	April 2013	0	70 ± 33	25 ± 35	7 ± 10	23 ± 20	14 ± 28
	June 2013	0	52 ± 41	32 ± 35	4 ± 10	20 ± 16	13 ± 28
FB (n=7)	April 2012	0	29 ± 30	0	0	18 ± 31	1 ± 2
	June 2012	0	6 ± 13	0	0	0	20 ± 45
	October 2012	0	13 ± 26	0	0	16 ± 28	1 ± 4
	December 2012	0	69 ± 38	0	0	20 ± 29	0
	February 2013	0	92 ± 6	6 ± 7	0	18 ± 17	0
	April 2013	0	81 ± 22	19 ± 22	0	20 ± 38	1 ± 4
	June 2013	0	91 ± 12	1 ± 4	0	34 ± 42	0
JZ (n = 6)	April 2012	17 ± 41	43 ± 44	0	5 ± 8	0	17 ± 17
	June 2012	13 ± 33	12 ± 18	0	0	0	10 ± 11
	October 2012	13 ± 33	12 ± 24	0	0	0	0
	December 2012	34 ± 45	64 ± 47	0	0	2 ± 4	8 ± 12
	February 2013	12 ± 29	87 ± 33	0	10 ± 24	24 ± 12	±
	April 2013	0	91 ± 12	4 ± 7	28 ± 29	32 ± 25	3 ± 6
	June 2013	3 ± 8	89 ± 9	0	22 ± 26	30 ± 28	4 ± 10
KB (n = 4)	April 2012	0	33 ± 43	50 ± 58	14 ± 14	0	0
	June 2012	0	36 ± 48	48 ± 55	15 ± 16	0	0
	October 2012	1 ± 3	48 ± 50	46 ± 54	10 ± 8		
	December 2012	0	46 ± 51	49 ± 56	9 ± 10	0	0
	February 2013	0	44 ± 49	49 ± 56	10 ± 12	0	0
	April 2013	0	41 ± 43	48 ± 55	14 ± 8	0	0
	June 2013	0	29 ± 35	45 ± 52	10 ± 12	0	0
MT (n = 3)	April 2012	50 ± 50	10 ± 10	40 ± 46	32 ± 39	0	48 ± 41
	June 2012	87 ± 13	7 ± 12	7 ± 8	28 ± 8	0	38 ± 25
	October 2012	65 ± 44	2 ± 3	30 ± 48	12 ± 20	0	50 ± 40
	December 2012	67 ± 42	3 ± 6	30 ± 44	27 ± 12	0	27 ± 21
	February 2013	80 ± 28	3 ± 4	13 ± 18	10 ± 14	0	30 ± 42
	April 2013	48 ± 46	3 ± 6	48 ± 45	25 ± 17	3 ± 6	20 ± 13
	June 2013	33 ± 58	2 ± 3	62 ± 54	27 ± 21	0	35 ± 26
MZ (n = 9)	April 2012	19 ± 28	33 ± 29	37 ± 35	11 ± 9	5 ± 8	45 ± 29
	June 2012	34 ± 31	29 ± 20	21 ± 19	11 ± 13	2 ± 5	36 ± 24
	October 2012	2 ± 5	40 ± 34	31 ± 36	11 ± 10	4 ± 8	14 ± 24
	December 2012	6 ± 11	36 ± 26	35 ± 35	16 ± 11	3 ± 7	32 ± 27
	February 2013	2 ± 4	36 ± 26	61 ± 26	8 ± 9	10 ± 7	36 ± 33
	April 2013	6 ± 12	36 ± 24	37 ± 34	12 ± 9	4 ± 7	38 ± 34
	June 2013	8 ± 12	45 ± 38	17 ± 19	13 ± 13	1 ± 2	34 ± 31
PF (n = 11)	April 2012	27 ± 37	37 ± 33	16 ± 28	8 ± 8	12 ± 17	35 ± 26
	June 2012	24 ± 31	36 ± 29	12 ± 14	3 ± 3	0	55 ± 40
	October 2012	19 ± 27	48 ± 36	13 ± 20	7 ± 8	7 ± 11	31 ± 26
	December 2012	40 ± 36	26 ± 35	25 ± 30	9 ± 10	2 ± 4	41 ± 33
	February 2013	30 ± 39	33 ± 30	26 ± 27	11 ± 13	5 ± 7	35 ± 32
	April 2013	11 ± 20	36 ± 27	31 ± 25	12 ± 13	1 ± 3	45 ± 35
	June 2013	1 ± 5	56 ± 33	15 ± 16	7 ± 9	1 ± 3	47 ± 32
SB (n = 6)	April 2012	20 ± 26	41 ± 32	15 ± 38	9 ± 15	4 ± 7	6 ± 11
	June 2012	16 ± 26	41 ± 33	16 ± 37	10 ± 18	3 ± 8	8 ± 11
	October 2012	24 ± 42	27 ± 39	14 ± 38	13 ± 13	±	9 ± 19
	December 2012	21 ± 37	42 ± 35	14 ± 38	7 ± 10	0	11 ± 20
	February 2013	13 ± 30	65 ± 39	14 ± 38	11 ± 13	0	11 ± 19
	April 2013	20 ± 35	46 ± 36	13 ± 34	13 ± 13	0	11 ± 20
	June 2013	6 ± 11	55 ± 36	14 ± 36	9 ± 11	0	11 ± 18
WS (n = 7)	April 2012	1 ± 4	61 ± 19	6 ± 15	7 ± 12	12 ± 15	13 ± 22
	June 2012	3 ± 8	45 ± 36	2 ± 4	7 ± 14	12 ± 22	10 ± 20
	October 2012	5 ± 9	70 ± 21	±	10 ± 20	1 ± 2	20 ± 20
	December 2012	0	89 ± 26	1 ± 2	11 ± 15	13 ± 19	8 ± 9
	February 2013	0	75 ± 32	11 ± 15	14 ± 20	8 ± 8	9 ± 21
	April 2013	3 ± 8	87 ± 13	10 ± 10	13 ± 19	11 ± 9	13 ± 26
	June 2013	3 ± 5	89 ± 18	9 ± 15	13 ± 19	18 ± 13	16 ± 28

Table 2.4 Means and standard deviations of water quality variables grouped by site cluster and sampling period. Number of sites in each cluster is given in parentheses. DO, dissolved oxygen; Temp, temperature; Sal, salinity.

Cluster	Sampling Period	pH	DO (mg.L^{-1})	Temp (°C)	Sal (psu)
ES (n=6)	April 2012	6.73 ± 1.19	6.50 ± 2.83	25.94 ± 3.86	2.61 ± 3.18
	June 2012	7.10 ± 1.19	9.74 ± 6.12	19.69 ± 1.44	1.16 ± 1.35
	October 2012	6.60 ± 0.72	6.62 ± 2.62	21.40 ± 1.65	2.27 ± 2.95
	December 2012	6.54 ± 0.67	5.29 ± 2.15	24.68 ± 0.30	3.42 ± 3.59
	February 2013	6.55 ± 0.62	3.50 ± 1.87	28.46 ± 2.12	1.49 ± 1.54
	April 2013	6.66 ± 0.48	5.86 ± 2.38	24.05 ± 2.01	2.05 ± 2.15
	June 2013	6.53 ± 0.67	7.07 ± 1.73	20.88 ± 1.58	4.20 ± 4.39
FB (n=7)	April 2012	7.65 ±031	9.39 ± 1.69	24.30 ± 4.96	16.04 ± 17.76
	June 2012	7.19 ±0.54	10.86 ± 1.65	19.48 ± 2.92	38.79 ± 25.01
	October 2012	8.06 ± 0.22	6.25 ± 1.68	29.77 ± 3.20	27.04 ± 15.52
	December 2012	8.13 ±d17	11.20 ± 3.52	32.31 ± 1.82	18.52 ± 8.52
	February 2013	8.13 ± 0.29	5.71 ± 0.52	28.84 ± 1.43	15.03 ± 4.80
	April 2013	7.90 ± 0.75	9.41 ± 1.58	18.59 ± 1.94	13.84 ± 5.74
	June 2013	8.41 ± 0.45	7.58 ± 0.86	18.50 ± 1.53	19.05 ± 4.79
JZ (n = 6)	April 2012	7.70 ± 0.27	7.87 ± 0.54	24.97 ± 1.74	0.10 ± 00.04
	June 2012	6.41 ± 0.48	13.17 ± 2.65	20.50 ± 2.60	0.09 ± 00.09
	October 2012	7.71 ± 0.11	5.53 ± 0.55	26.53 ± 2.98	0.20 ± 0.06
	December 2012	7.58 ± 0.26	8.19 ± 1.64	29.33 ± 2.15	0.15 ± 00.02
	February 2013	7.44 ± 0.42	3.39 ± 1.76	26.46 ± 1.86	0.13 ± 00.03
	April 2013	7.20 ± 0.41	5.89 ± 3.04	22.71 ± 1.99	0.13 ± 00.03
	June 2013	7.85 ± 0.66	8.29 ± 0.78	17.02 ± 4.33	0.14 ± 00.01
KB (n = 4)	April 2012	7.64 ± 0.76	10.41 ± 3.25	25.11 ± 2.34	0.86 ± 10.40
	June 2012	6.27 ± 0.58	13.49 ± 1.97	16.17 ± 2.23	0.77 ± 10.29
	October 2012	7.91 ± 0.71	6.29 ± 0.70	24.49 ± 0.37	0.92 ± 1.43
	December 2012	8.24 ± 0.83	10.78 ± 1.37	28.29 ± 1.00	0.51 ± 00.52
	February 2013	8.42 ± 0.85	7.34 ± 1.24	29.33 ± 0.18	0.86 ± 10.25
	April 2013	7.50 ± 0.43	9.30 ± 1.90	23.01 ± 0.83	1.09 ± 1.68
	June 2013	7.85 ± 0.60	8.56 ± 0.79	19.88 ± 0.69	1.12 ± 1.75
MT (n = 3)	April 2012	8.11	7.40	21.98	0.30
	June 2012	6.74	4.26	17.93	0.26
	October 2012	8.26	9.06	27.34	0.52
	December 2012	7.87	4.65	25.44	0.55
	February 2013	8.21	1.55	27.45	0.46
	April 2013	7.59	2.90	20.47	0.64
	June 2013	8.79	7.45	19.78	0.56
MZ (n = 9)	April 2012	7.17 ± 0.42	8.05 ± 1.48	25.36 ± 2.18	0.51 ± 00.36
	June 2012	6.48 ± 0.58	24.79 ± 12.59	18.25 ± 3.87	0.34 ± 00.24
	October 2012	7.53 ± 0.31	5.85 ± 1.23	26.09 ± 2.17	0.43 ± 0.23
	December 2012	7.50 ± 0.28	8.22 ± 2.29	27.45 ± 2.13	0.45 ± 00.18
	February 2013	7.45 ± 0.25	5.80 ± 5.54	27.58 ± 2.57	0.32 ± 00.12
	April 2013	7.14 ± 0.42	8.56 ± 1.23	24.31 ± 4.04	0.43 ± 00.26
	June 2013	7.92 ± 0.44	7.37 ± 1.74	20.71 ± 2.63	0.58 ± 00.35
PF (n = 11)	April 2012	6.96 ± 0.59	9.05 ± 2.83	24.54 ± 3.46	0.75 ± 00.84
	June 2012	6.66 ± 0.40	11.92 ± 4.53	18.30 ± 3.73	20.12 ± 50.29
	October 2012	7.13 ± 0.35	5.70 ± 1.26	28.18 ± 3.85	0.58 ± 0.39
	December 2012	7.02 ± 0.26	10.16 ± 1.78	27.69 ± 1.19	0.50 ± 00.37
	February 2013	7.72 ± 0.55	5.28 ± 1.95	30.51 ± 2.52	0.34 ± 00.15
	April 2013	7.41 ± 0.34	6.82 ± 2.37	25.22 ± 3.49	0.45 ± 00.35
	June 2013	7.41 ± 0.59	8.67 ± 0.85	18.81 ± 3.76	0.52 ± 00.39
SB (n = 6)	April 2012	7.91 ± 0.64	11.75 ± 2.95	24.42 ± 1.63	0.19 ± 00.08
	June 2012	7.16 ± 0.90	12.37 ± 1.65	20.59 ± 2.18	0.22 ± 00.12
	October 2012	8.22 ± 0.73	6.44 ± 1.63	24.44 ± 0.87	0.33 ± 0.08
	December 2012	8.44 ± 0.82	13.24 ± 6.81	29.07 ± 2.49	0.39 ± 00.09
	February 2013	8.26 ± 0.43	6.12 ± 1.99	27.29 ± 1.04	0.38 ± 00.09
	April 2013	8.50 ± 0.86	10.08 ± 4.92	23.26 ± 2.15	0.35 ± 00.09
	June 2013	8.30 ± 0.90	8.15 ± 2.00	17.84 ± 1.36	0.35 ± 00.09
WS (n = 7)	April 2012	7.14 ± 0.80	8.49 ± 3.25	25.45 ± 4.02	3.22 ± 3.14
	June 2012	6.19 ± 0.43	6.83 ± 2.06	19.31 ± 2.12	7.91 ± 9.61
	October 2012	7.40 ± 0.67	6.17 ± 1.25	24.76 ± 3.32	3.43 ± 2.99
	December 2012	7.58 ± 0.74	8.85 ± 3.88	23.73 ± 1.98	3.93 ± 4.20
	February 2013	7.20 ± 0.67	4.00 ± 1.48	28.52 ± 1.45	2.32 ± 3.04
	April 2013	7.50 ± 0.54	6.79 ± 1.77	20.33 ± 0.96	5.00 ± 4.26
	June 2013	7.49 ± 0.50	6.92 ± 0.72	20.97 ± 1.16	5.74 ± 4.18

Table 2.5 Means and standard deviations of monthly rainfall at three lag periods grouped by site cluster and sampling period. Standard deviations are missing from clusters in which rainfall data were gathered from one rainfall station for all sites. Number of sites in each cluster is given in parentheses.

Cluster	Sampling Period	Rain 1	Rain 2	Rain 3
ES (n=6)	April 2012	418 ± 26	78 ± 10	99 ± 29
	June 2012	23 ± 3	15 ± 17	418 ± 26
	October 2012	229 ± 32	9 ± 4	9 ± 11
	December 2012	81 ± 9	176 ± 47	229 ± 32
	February 2013	162 ± 53	101 ± 43	81 ± 9
	April 2013	76 ± 9	157 ± 6	162 ± 53
	June 2013	49 ± 6	69 ± 25	76 ± 9
FB (n=7)	April 2012	24	69	8
	June 2012	4	13	24
	October 2012	255	2	0
	December 2012	42	94	255
	February 2013	72	89	42
	April 2013	50	89	72
	June 2013	10	20	50
JZ (n = 6)	April 2012	66	140	51
	June 2012	34	4	66
	October 2012	173	0	0
	December 2012	40	111	173
	February 2013	96	40	40
	April 2013	70	12	96
	June 2013	9	36	70
KB (n = 4)	April 2012	290	102	60
	June 2012	4	34	290
	October 2012	277	0	16
	December 2012	109	50	277
	February 2013	330	19	109
	April 2013	44	11	330
	June 2013	6	81	44
MT (n = 3)	April 2012	237	58	36
	June 2012	12	25	237
	October 2012	249	12	14
	December 2012	96	163	249
	February 2013	222	170	96
	April 2013	115	118	222
	June 2013	6	37	115
MZ (n = 9)	April 2012	115	82	51
	June 2012	2	13	115
	October 2012	191	4	0
	December 2012	23	63	191
	February 2013	128	72	23
	April 2013	24	4	128
	June 2013	7	42	24
PF (n = 11)	April 2012	110 ± 17	62 ± 9	94 ± 1
	June 2012	27 ± 12	11 ± 6	110 ± 17
	October 2012	169 ± 42	1 ± 1	1 ± 1
	December 2012	62 ± 15	111 ± 19	169 ± 42
	February 2013	148 ± 21	95 ± 14	62 ± 15
	April 2013	43 ± 33	35 ± 39	148 ± 21
	June 2013	6 ± 5	29 ± 13	43 ± 33
SB (n = 6)	April 2012	262 ± 39	149 ± 15	51 ± 5
	June 2012	39 ± 13	14 ± 8	262 ± 39
	October 2012	273 ± 17	5 ± 3	12 ± 13
	December 2012	87 ± 12	145 ± 6	273 ± 17
	February 2013	225 ± 55	133 ± 18	87 ± 12
	April 2013	38 ± 4	37 ± 2	225 ± 55
	June 2013	17 ± 2	35 ± 5	38 ± 4
WS (n = 7)	April 2012	315 ± 16	74 ± 1	83 ± 14
	June 2012	11 ± 4	22 ± 3	313 ± 16
	October 2012	193 ± 35	13 ± 6	3 ± 3
	December 2012	69 ± 6	165 ±	193 ± 35
	February 2013	141 ± 39	105 ± 41	69 ± 6
	April 2013	72 ± 14	124 ± 27	141 ± 39
	June 2013	17 ± 6	50 ± 5	72 ± 14

Table 2.6 Means and standard deviations of proportion of land cover classes in a 3 km buffer around sampling sites, grouped by site cluster. ANTHRO, anthropogenically modified land cover; NAT, natural vegetation; WET, estuarine and freshwater cover. Number of sites in each cluster is given in parentheses.

Cluster	ANTHRO	NAT	WET
ES (n = 6)	21.4 ± 12.5	34.1 ± 13.6	41.7 ± 16.4
FB (n = 7)	28.1 ± 14.3	34.6 ± 16.1	37.3 ± 24.3
JZ (n = 6)	5.1 ± 7.0	40.8 ± 28.9	27.2 ± 26.1
KB (n = 4)	23.4 ± 11.6	44.4 ± 16.1	19.4 ± 24.8
MT (n = 3)	61.1 ± 7.0	26.3 ± 7.4	12.6 ± 3.6
MZ (n = 9)	30.8 ± 16.4	53.8 ± 20.2	15.4 ± 9.4
PF (n = 11)	42.4 ± 32.7	42.6 ± 28.0	14.7 ± 16.0
SB (n = 7)	16.2 ± 11.6	43.1 ± 16.0	26.9 ± 27.1
WS (n = 7)	44.2 ± 22.3	27.3 ± 7.1	28.5 ± 19.3

3 DO FORAGE-PREDATION TRADE-OFFS DRIVE HABITAT SELECTION BY SEMI-NOMADIC WATERBIRDS?

3.1 Abstract

The choices that animals make about where and when to occupy particular habitats have profound implications for their survival. Habitat choice is poorly understood for long-lived animals in semi-arid environments, where both resources and risks can be highly variable and animals must balance a range of different habitat and life history needs. Functional responses (i.e., use that depends on availability) are predicted to occur when animals must choose between habitats that provide contrasting resources, such as quality forage versus safety from predators, but have not been previously documented for waterbirds. I used satellite telemetry data from two different populations of the semi-nomadic Egyptian Goose *Alopochen aegyptiaca* to address: (1) how habitat selection for habitat types varied across seasons, sites, and life-stages; (2) whether Egyptian Geese showed functional responses in habitat use; and (3) whether functional responses related to trade-offs between predation risk and forage quality at the home-range scale. Egyptian Geese face a trade-off between using wetlands, which are safer but offer lower quality forage, and agricultural land, which provides highly nutritious forage but with higher levels of predation. My results showed that birds in both populations strongly selected wetlands and agricultural habitats throughout the year, although the magnitudes of selection coefficients differed between seasons. There was a negative functional response, with selection for both wetlands and agricultural habitats decreasing as their availability increased. At the home-range scale, both forage optimisation and predation risk were limiting factors. In addition to providing the first demonstration of a functional response by waterbirds in a semi-arid environment, my results have important implications for understanding the fitness consequences of trade-offs made by nomadic animals.

3.2 Introduction

Fundamental to the ecological understanding of any organism is knowledge of both its habitat needs and habitat use. Insights into the mechanisms that drive habitat selection provide important information about the determinants of individual fitness and the ways in which animals meet their requirements for survival and reproduction (Rosenzweig 1981, Manly et al. 2002, Gaillard et al. 2010). To maximise their fitness potential, animals should prioritise the use of habitats that provide at least the minimum quantity of a limiting resource or condition (Morellet et al. 2011).

One of the underlying assumptions in traditional habitat selection studies was that animals use a constant amount of a habitat independently of its proportional availability (Aebischer et al. 1993). Selection was inferred when the ratio of used habitat units to available units was greater than one, and avoidance when the ratio was less than one. In recent years, however, this approach has been questioned. Mysterud & Ims (1998) proposed that in situations where trade-offs occur between using two contrasting resource types, the strength of habitat selection for a certain habitat may be dependent on its proportional availability. The dependence of habitat selection on habitat quantity is an example of a functional response in habitat selection (with strong parallels to the functional responses of predators to variations in the relative abundances of prospective prey species; Holling & Buckingham 1976). An example of a habitat quality trade-off is the differential use of two spatially segregated habitat patches which provide either safety from predators or quality forage (Hebblewhite and Merrill 2009).

Functional responses are likely to occur when no single habitat provides access to all the necessary resources (Mysterud and Ims 1998, Massé and Côté 2009, Godvik et al. 2009). If a habitat provides a limiting resource it is expected that selection for this habitat will increase as it becomes scarcer, which will result in a negative functional response. Recent studies have explored functional responses in habitat selection across a variety of taxa: e.g., Polar bears (Mauritzen et al. 2003); Moose (Osko et al. 2004, Herfindal et al. 2009, Mabille et al. 2012); Forest songbirds (Gillies & St. Clair 2010); Reindeer (Hansen et al. 2009); and Roe deer (Pellerin et al. 2010, Morellet et al. 2011). These studies have used variation in functional responses to test a range of ecological hypotheses about such things as seasonal variations in environmental conditions, home range size, ideal free distributions, habitat

switching, substitutable habitats, and scale specific trade-offs between forage optimisation and predation risk.

Studies of large herbivores have found that at the landscape scale, safety is a limiting factor and animals select habitats that best provide cover, while at the home range scale they seek to maximise forage quality and select food-rich habitats (Dussault et al. 2005, although see Herfindal et al. 2009). Other studies (Hebblewhite and Merrill 2009, Godvik et al. 2009, Mabille et al. 2012) have also examined the forage-predation trade-off; however, methods using functional responses to do so have not been applied to highly mobile or semi-nomadic species living in environments that are not strongly seasonal. While much attention has been paid to direct effects of predation in breeding birds (reviewed in Lima 2009), the importance of non-lethal effects of predation (also termed 'trait-mediated' effects; Lima 1998) in birds has recently been recognised and may lead to fitness consequences such as reduced reproductive output, reduced foraging rates and sub-optimal body condition (Cresswell 2008). Behavioural responses to non-lethal effects are likely to be well developed in birds because of their ability to escape predation risk via flight and their well-developed cognitive abilities. Simply measuring predator density or mortality rates is not enough to fully understand and model the costs associated with predation risk. Assessing the problem through a foraging-predation trade-off framework has the potential to better explain the influence of predation risk on population and community dynamics (Bolker et al. 2003, Cresswell 2008).

Here I focus on understanding broad-scale habitat choice in relation to the movements of waterfowl in southern Africa. The recent development of lightweight GPS devices has allowed researchers to obtain fine-scale movement data which are of high accuracy over long temporal scales (Tomkiewicz et al. 2010). This is particularly relevant for understanding waterfowl habitat use because waterfowl are highly mobile and can perform rapid movements over broad spatial scales (Roshier et al. 2008a). Much of our knowledge about waterfowl ecology comes from studies in temperate regions in the northern hemisphere (Owen and Black 1990, Baldassarre and Bolen 2006); telemetry studies on waterfowl movements in arid or tropical landscapes are still relatively scarce. Previous research in these systems has primarily analysed properties of movement trajectories: e.g., maximum and daily distance, movement rates, and movement path tortuosity (Roshier et al. 2008a, 2008b, Traill et al. 2010, Gaidet et al. 2010, Cumming et al. 2012a, Ndlovu et al. 2013). Although these studies

have contributed to our understanding of waterfowl movement, none has tested for habitat selection or functional responses within a Resource Selection Function (RSF) framework.

I used RSFs to explore habitat selection of GPS-tagged Egyptian Geese *Alopochen aegyptiaca* tracked for 12 months in two contrasting landscapes within South Africa. Inferences about habitat selection depend on the scales at which use and availability are measured (Johnson 1980, Mayor et al. 2009). Four hierarchical orders of selection (species range, home range, habitat patch, resource item) have been proposed for other organisms. It has been suggested that periods of analysis for habitat selection should be kept short to control for changes in underlying resources (Manly et al. 2002), so here I focus on monthly selection at the home range scale.

Egyptian Geese have an extensive species range across sub-Saharan Africa. Results of ringing recoveries suggest widespread movement, with records showing dispersal distances of over 1000km (Underhill et al. 1999). Egyptian Geese prefer freshwater wetlands with open shorelines, although they have also been to found to inhabit virtually all forms of water bodies including estuaries, sewage works, harbours and offshore islands (Milstein 1993, Underhill and Kemper 2000). Egyptian Geese are primarily grazers and in recent years have thrived in human modified landscapes such as those characterised by agricultural land (favouring mainly cereal crops), golf courses, parks, and lawns in urban areas. Recent patterns of range expansion, especially into south-eastern South Africa, have been attributed to the increase in abundance of these anthropogenic habitats (Okes et al. 2008), whereas historically Geese were probably restricted to flood plains and large rivers with extensive sandbanks (Hockey et al. 2005).

I first identified habitats that were actively selected and tested whether selection was influenced by annual life-stages (internal factors), season, or site (external factors). Second, I investigated the foraging-predation trade-off hypothesis in habitat selection by relating individual variation in habitat selection to the relative availability of habitat types. By focusing on functional responses at the home range scale, I tested whether geese prioritise habitats which provide lower risk of predation or those which allow them to optimise foraging intake. More generally, I also explored whether current RSF methods were appropriate for detecting trade-offs in highly mobile animal moving at broad scales across the landscape.

3.3 Methods

I first tested whether variation in selection for five habitat categories (wetlands, cultivated land, natural vegetation, degraded land, and urban built-up land) was influenced by internal or external factors (Nathan et al. 2008), or a combination of both. Internal factors relate to habitat requirements through the annual cycle of Egyptian Geese, which can be separated into three periods: moulting (flightless period when primary and secondary feathers are synchronously shed), breeding, and ranging (periods outside of moult or breeding). Habitat choice is influenced by risk of predation, forage quality, availability of roost/loafing/nesting sites, and availability of permanent wetlands when moulting. I expected to observe variation in habitat selection through different life stages as a result of Egyptian Geese balancing these needs.

External factors relate to the availability of resources through different seasons. In southern Africa, seasons are determined more by rainfall than temperature (Tyson and Preston-Whyte 2000). If external factors play a more prominent role in habitat use, I would expect habitat selection to differ as landscape productivity varies between wet and dry seasons. Furthermore, I explored whether patterns of habitat selection differed between the two study areas, where geese were exposed to different landscape conditions.

To investigate the foraging-predation trade-off in habitat selection I determined whether Egyptian Geese showed a functional response, and if so, in which habitats this occurred. Wetland habitats provide safety from predators as well as roost sites, while cultivated land can provide highly nutritious food source in the form of seeds and spilled grain. If food quality is a limiting factor at the home range scale, I would expect to see a negative functional response in selection for cultivated land (i.e. selection increases as availability decreases). If safety from predators is more important, I would expect to see a negative functional response in selection for wetlands.

3.3.1 Site and study population

Despite their common name, Egyptian Geese *Alopochen aegyptiaca* (Linnaeus) are in fact shelducks from the subfamily Tadorninae. The Egyptian Geese in my study population originated from two South African sites (Figs. 3.1 & 3.2): Strandfontein wastewater treatment works in the Western Cape Province and Barberspan Nature Reserve in the North-West Province. See Chapter 2 for site descriptions and capture protocol. To analyse the effect of

rainfall seasonality on habitat selection, each month of the study period was assigned as either wet or dry, depending on the site (Strandfontein wet and Barberspan dry: April to September; Strandfontein dry and Barberspan wet: October to March). Individuals from both study populations did not move into differing rainfall regions during the study period (see Figs. 3.1 & 3.2 for movement paths).

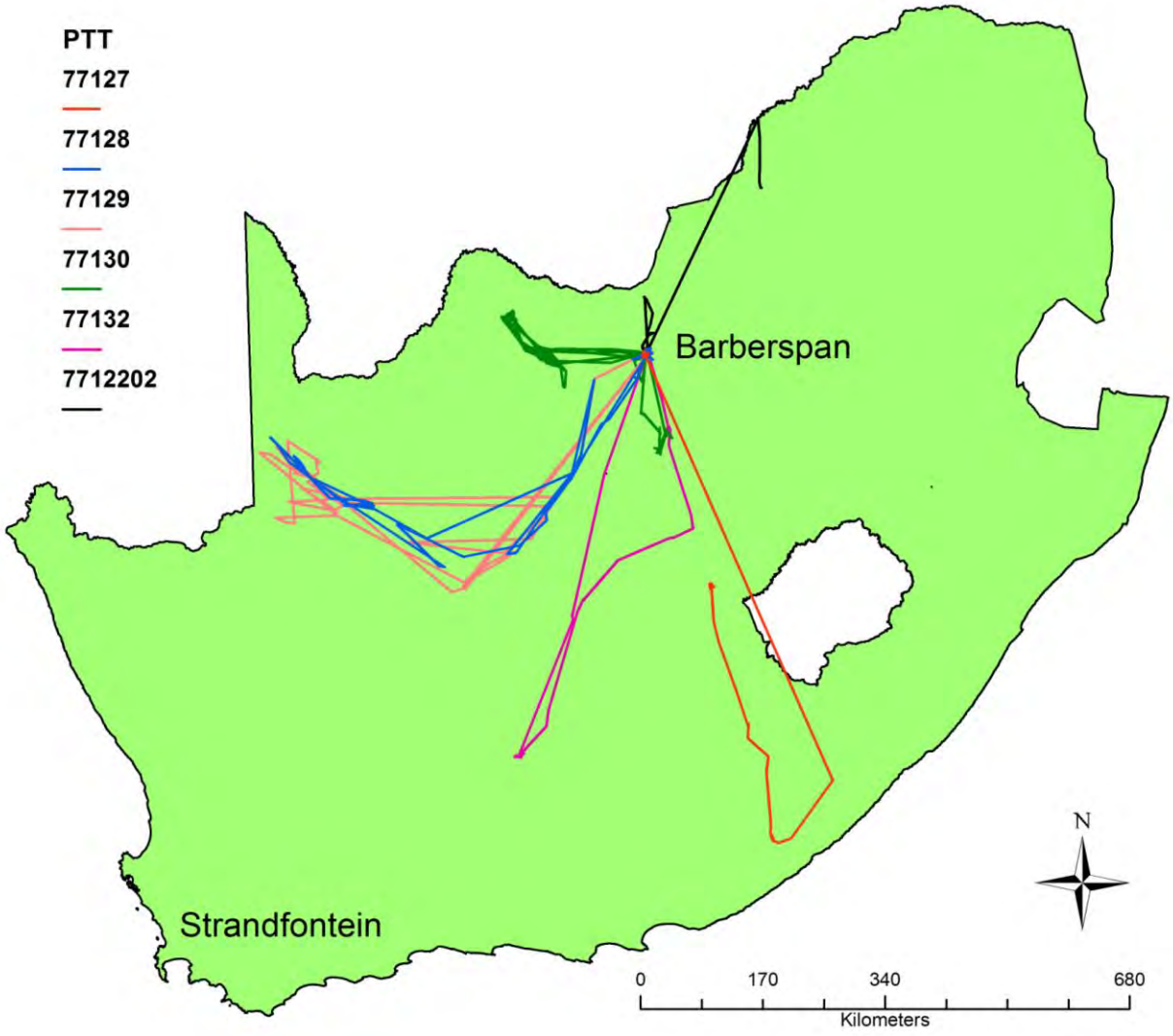


Figure 3.1 Map showing the movement paths over the study period of Egyptian Geese (n = 6) tagged at Barberspan, South Africa. PTT, transmitter identity.

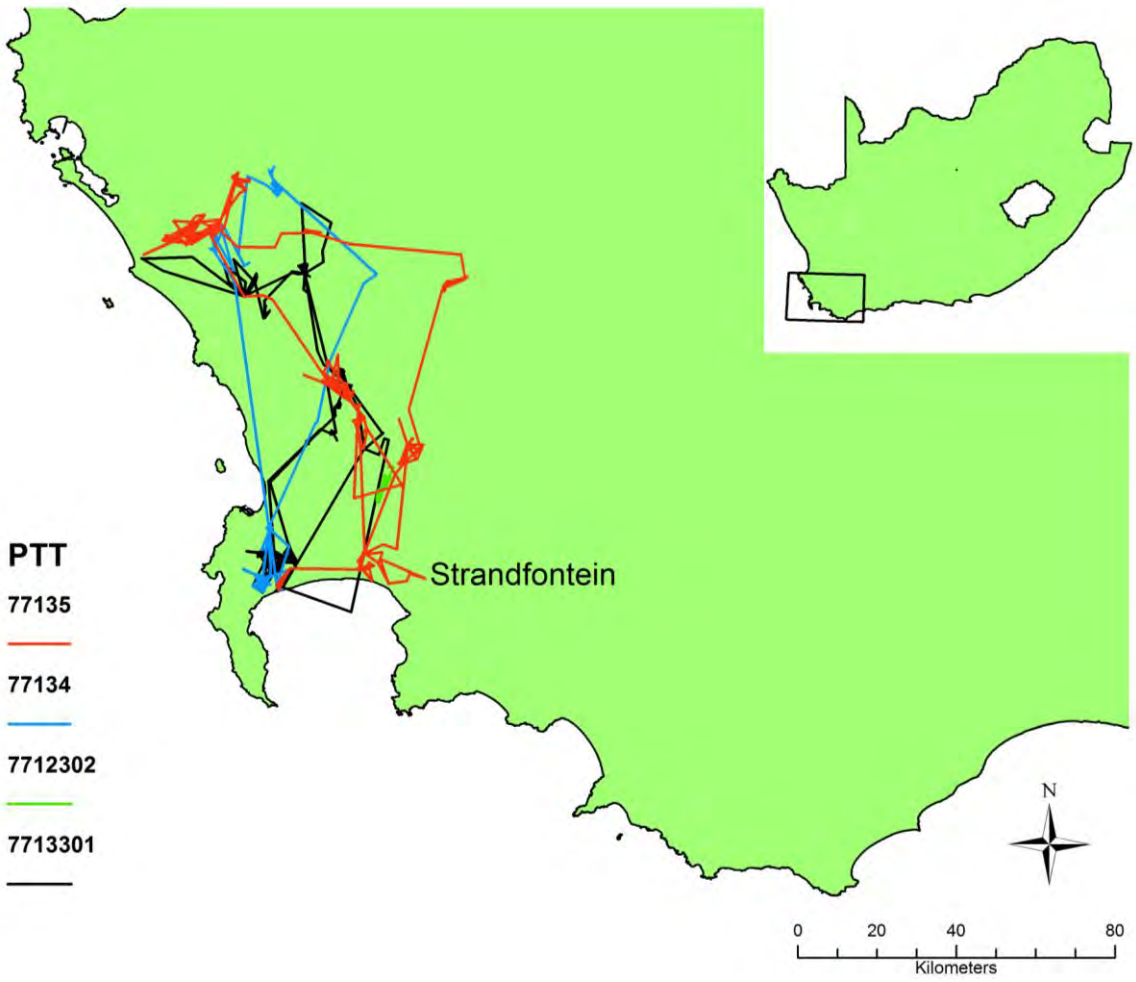


Figure 3.2 Map showing the movement paths over the study period of Egyptian Geese (n = 4) tagged at Strandfontein, South Africa. PTT, transmitter identity.

The annual cycle of Egyptian Geese can be separated into three life stages: breeding, moulting and ranging. In total, breeding takes between 90 and 100 days (ca. 28 days of incubation plus ca. 75 days for ducklings to fledge; Milstein 1993). Egyptian Geese undergo a period of flightless moult of ca. 40 days when primary and secondary feathers are synchronously shed (Milstein 1993). Ranging periods occur outside of breeding and moulting and there is strong evidence for moult migration in this species (Cumming et al. 2012a). To assess the effect of life stage on habitat selection, I created an annual timeline of these three periods. This was done by combining information on peak breeding and moulting periods from published sources (Milstein 1993, Little et al. 1995, Hockey et al. 2005, Ndlovu 2012) with an analysis of monthly averages of daily movement distances. Compared with ranging periods, distances moved during breeding and moulting were low. I could be sure of initial

moult periods because only birds that had just finished flightless moult were tagged. During breeding, birds are constrained to intermediate distance movements by the need to return to the nest and by the distances that ducklings can walk. The longest movements were during periods of ranging and moult migration. Daily distances were calculated from the telemetry data (see below) by the summation of distances between GPS relocations for the entire day. Separate calculations were performed on birds from Barberspan and Strandfontein (Fig. 3.3 & 3.4 respectively).

3.3.2 Telemetry and habitat data

To characterise habitat use throughout one calendar year, individuals that were successfully tracked for at least 11 months of the year were considered in the analysis. Data from birds that moved out of South Africa during the study period were also discarded because land cover maps between South Africa and neighbouring countries were not standardised and therefore not comparable. These exclusions left sample sizes of four and six geese tagged at Strandfontein and Barberspan, respectively (Table 3.1).

Individual monthly home ranges were delineated by 95% isopleths (with ad-hoc smoothing parameter) using the kernelUD function in the adehabitatHR package (Calenge 2006) in R for windows version 3.0.2 (R Core Team 2013). Kernel Density Estimator methods were chosen because they have been shown to outperform traditional minimum convex polygon methods and LoCoH (Börger et al. 2006, Cumming and Cornélis 2012). Home ranges were then overlaid onto the 2009 South African National Land Cover (NLC) raster map (SANBI 2013).

The resolution of the 2009 NLC map is 30 x 30m and habitats are classed as Natural, Cultivated, Degraded, Water bodies, Plantations, Mines, or Urban Built-Up. The 2009 NLC map is an update from a national land cover map that was produced in 2000. The original map consisted of 49 classes, which were subsequently condensed into the seven classes mentioned above (Appendix 1). Mines and Plantations were rarely used by birds and were subsequently excluded from further analyses. Habitat use was measured by extracting a categorical habitat value for each GPS relocation, and availability for each habitat was measured by totalling the number of habitat pixels within a given home range. Keeping in mind that Egyptian Geese have discontinuous home ranges (Cumming *et al.* 2012), 117 home range polygons based on 25,116 relocations were included in the analysis.

Table 3.1 Details of individual GPS-tagged Egyptian Geese. Start and end date refers to the time period of tracking data used in the study. Total fixes are the number of relocations recorded over the study period, while mean monthly fixes are the total number of r relocations divided by the number of months the transmitter was active. PTT, transmitter identity; BAR, Barberspan; STR, Strandfontein.

PTT	Site	Sex	Start date	End date	Total Fixes	Mean monthly fixes (± SD)
7712202	BAR	Male	07/06/2008	30/05/2009	883	220 ± 51
7712302	STR	Male	04/12/2008	13/11/2009	1194	132 ± 151
77127	BAR	Male	07/06/2008	31/05/2009	3323	276 ± 34
77128	BAR	Female	07/06/2008	20/05/2009	3303	275 ± 73
77129	BAR	Male	07/06/2008	11/05/2009	2775	252 ± 81
77130	BAR	Male	07/06/2008	31/05/2009	2032	203 ± 126
77132	BAR	Female	07/06/2008	30/05/2009	2577	214 ± 100
7713301	STR	Male	04/12/2008	25/11/2009	2201	200 ± 124
77134	STR	Female	04/12/2008	31/12/2009	3192	266 ± 91
77135	STR	Male	04/12/2008	31/12/2009	3906	325 ± 17

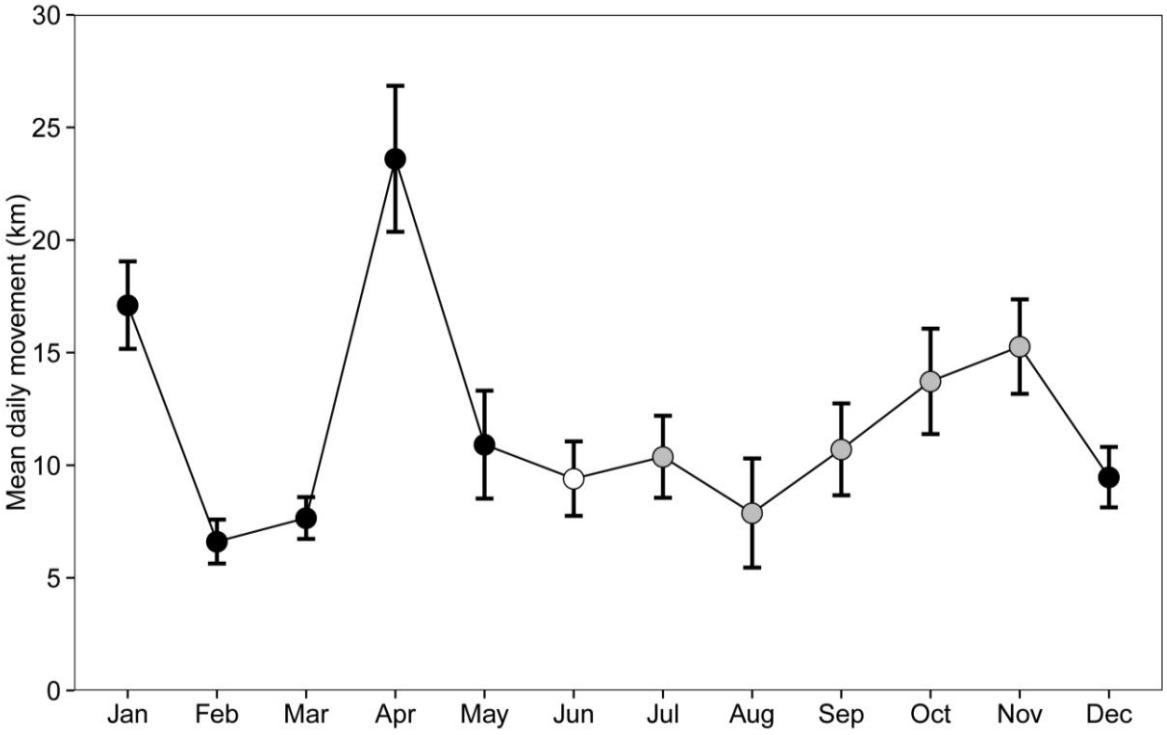


Figure 3.3 Mean and standard errors of daily movement distance (km) for Egyptian Geese tagged at Barberspan over the study period. Colour of points represents life stages (black, ranging; grey, breeding; white, moulting).

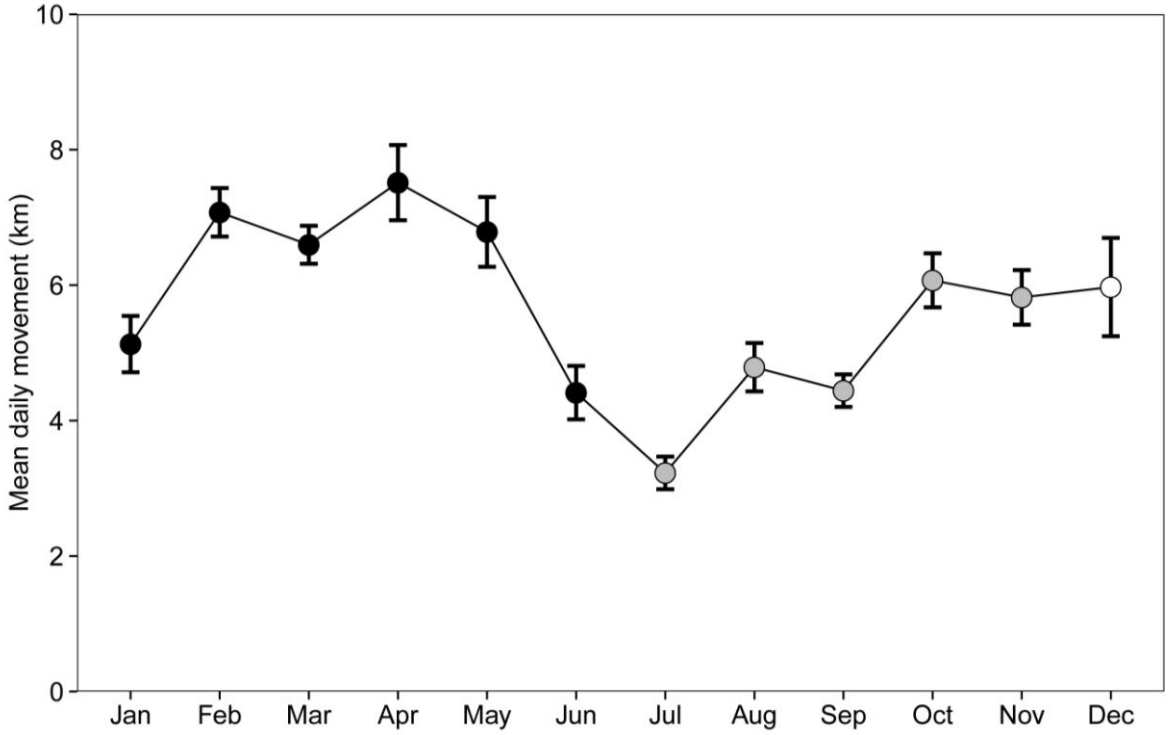


Figure 3.4 Mean and standard errors of daily movement distance (km) for Egyptian Geese tagged at Strandfontein over the study period. Colour of points represents life stages (black, ranging; grey, breeding; white, moulting).

3.3.3 Habitat selection

My analysis of habitat selection at the home range scale (3rd order selection; Johnson 1980) corresponds to a type III design, where use and availability are measured for each individual (Manly et al. 2002, Thomas and Taylor 2006). Resource selection functions (RSFs) were used to model habitat selection. To estimate RSFs, I followed the method in Herfindal *et al.* (2009) using Poisson log-linear models belonging to the class generalised linear mixed-effects models (GLMMs; Manly *et al.* 2002). The dependent variable of the model was the number of individual monthly relocations in habitat *j* within a monthly home range. A total of 72 and 45 monthly home range polygons were derived for Barberspan and Strandfontein individuals respectively. Within habitat *j* the number of relocations ranged from 0-298 (Barberspan) and 0-345 (Strandfontein). The dependent variable was then modelled as a function of site, habitat type, life-stage, and rainfall season. The resulting sample size was 585 (117 home range polygons x 5 habitat categories). Proportional availability of habitat *j* was added as an offset variable to approximate the expected number of relocations for an individual in habitat *j*. Once the offset variable had been incorporated, selection for a habitat *j* could be inferred from the parameter estimates of the fitted model. No selection for habitat *j* would be indicated by parameter estimates equal to the average expected number of relocations per habitat type from the combined set of monthly observations. This average value was determined by the intercept parameter of a null model, which included only the random effect and offset variable, and provided the estimate of expected number of relocations within a habitat of random size. In my null model this value was 0.974. By subtracting the average value from the estimated selection parameters of subsequent fitted models, positive selection or avoidance of a habitat could be inferred by selection parameters greater or less than zero respectively. Individual birds were added as random effects to all models (n = 10). This technique, which has been widely used (e.g. Gillies & St. Clair 2010; van Beest *et al.* 2010; Morellet *et al.* 2011), allowed us to control for the differing number of monthly individual relocations, draw population level inferences of habitat selection, and improve model fit by incorporating individual level variation in habitat selection (Gillies et al. 2006).

The first part of the analysis examined how the categorical variables of life stage, rainfall and site affected strength of selection for each habitat type. I fitted a suite of nested GLMMs starting from the most complex to simplified combinations of the full model. The full model included all the two-way interactions between habitat and each of the covariates.

Subsequent models included combinations of all the interactions, a model with habitat as the only covariate and a null model (i.e. no habitat selection). I used the second order Akaike's Information Criteria (AICc; Burnham & Anderson 2002) and the AICc weights to evaluate and select the model with the most support. Models with $\Delta AICc \leq 2$ were considered equivalent, in which case the most parsimonious model was chosen (Burnham and Anderson 2002).

The second part of the analysis examined the question of functional response (i.e. whether the strength of selection for a given habitat was dependent on the proportional availability of that habitat). The two-way interaction between proportional availability and habitat was added to the model with the most support from the first part of the analysis. The two models were then compared using a chi-squared test based on differences in log-likelihood. The second model was kept and used to infer a functional response if it provided a significantly better fit than the first model. All models were fitted with maximum likelihood using the glmer function in the R package lme4 (Bates et al. 2014). To control for over-dispersion in the data, an additive dispersion term was added as a random effect variable to all models (Nakagawa and Schielzeth 2013). To visualise the effects from the retained models, parameter estimates were plotted along with their 95% confidence intervals after posterior re-sampling (n = 5000 iterations) of estimates using the *sim* function in the R package arm (Gelman and Su 2013). Significance of parameters from the fitted model was achieved if the 95% confidence interval did not include zero. In addition to standard model diagnostics, model fit was evaluated by calculating $R^2_{GLMM\ (m)}$ (marginal variance explained by the fixed effects) and $R^2_{GLMM(c)}$ (conditional variance explained by the full model including random effects) following methods recently developed by Nakagawa & Schielzeth (2013).

3.4 Results

3.4.1 Habitat selection

In the analysis of monthly habitat selection of Egyptian Geese at the home range scale, the most parsimonious model with the best fit included the two-way interactions between habitat type and rainfall, and habitat type and site (Table 3.2). Model 1 therefore has the greatest support and suggests variation in patterns of habitat selection were best explained by study sites and rainfall seasons. In the chosen model (Table 3.3), the variance explained by the fixed effects was 46.8%, while the addition of the random effects increased the explained

variance to 47.1% (Table 3.2). This suggests both that the model provides a reasonable fit to the data, and that individual level variation in selection of habitat is fairly low among the study population. Selection for wetland habitat was pronounced at both sites during both seasons (Fig. 3.5), although Barberspan Egyptian Geese consistently showed greater selection than Strandfontein geese. Cultivated land was also positively selected during both seasons at Strandfontein and during the wet season at Barberspan. Degraded and urban built-up lands were actively avoided by birds at both sites throughout the year. Selection for natural habitat was positive in the wet seasons, although this pattern was not significant. Although there were differences in magnitude, seasonal selection patterns were markedly consistent between sites. Habitat selection at both sites was always highest in the wet season for natural, cultivated, and degraded land. The opposite response was evident in the wetland and urban habitats, where selection was consistently higher in the dry season (Fig. 3.5).

3.4.2 Functional response

A model testing for functional responses in habitat selection was created by adding the two-way interaction between habitat and proportional availability to model 1. The results of the log likelihood test suggested that adding proportional availability to model 1 significantly increased the model fit ($\chi^2 = 121.31$, df = 5, $p < 0.001$). The variance explained by the model including only the fixed effects was 60.1%, while the variance explained by the full model (including random effects) was 61.2%, which suggested a reasonable fit to the data. The combined effect across sites showed that Egyptian Geese exhibit a functional response in habitat selection (Figs 3.6 & 3.7). Selection for cultivated and wetland habitat significantly decreased with increasing availability of these habitats during both seasons, providing evidence for a negative functional response (Fig. 3.6). The response for cultivated habitat was strongest in the wet season, while that for wetland habitat was strongest in the dry season. This was consistent with the magnitude of selection in Figure 3.5. By contrast, a positive functional response was found in the remaining natural, degraded and urban built-up habitats (Fig. 3.7).

Table 3.2 Candidate set of generalised linear mixed models used to investigate the effect of habitat, site, rainfall season and life stage on variation in habitat selection of Egyptian Geese at the home range scale. Candidate models were based on a sample size of n = 585 (117 home range polygons x 5 habitat categories). Individual identity of Egyptian Geese was included as a random effect in all models. Models are ranked based on differences in the corrected Akaike's Information Criteria (ΔAICc) and Akaike weights (w_i). K is the number of estimated parameters and x represents an interaction between two variables. R^2 values are measures of model fit based on fixed effects only (marginal variance, $R^2_{GLMM(m)}$) and on the full model including random effects (conditional variance, $R^2_{GLMM(c)}$).

Model		AICc	K	ΔAICc(w_i)	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$
1	Habitat + rainfall + site + habitat x rainfall + habitat x site	3540.97	17	0.00 (0.61)	0.468	0.471
2	Habitat + rainfall + site + life stage + habitat x rainfall + habitat x site + habitat x life stage	3542.73	27	1.76 (0.25)	0.489	0.494
3	Habitat + rainfall + habitat x rainfall	3544.32	12	3.35 (0.11)	0.452	0.454
4	Habitat + rainfall + life stage + habitat x rainfall + habitat x life stage	3547.38	22	6.41 (0.02)	0.471	0.475
5	Habitat + site + life stage + habitat x site + habitat x life stage	3561.94	22	20.97 (0.00)	0.465	0.470
6	Habitat + site + habitat x site	3563.85	12	22.88 (0.00)	0.440	0.443
7	Habitat + life stage + habitat x life stage	3566.04	17	25.07 (0.00)	0.448	0.451
8	Habitat	3567.63	7	26.66 (0.00)	0.420	0.422
9	Intercept	3849.08	3	308.12 (0.00)		

Table 3.3 Summary of the generalised mixed effects model with the highest support for habitat selection by Egyptian Geese as a function of site and rainfall season. Confidence intervals were estimated from posterior re-sampling of parameter estimates. STR, Strandfonetin; BAR, Barberspan.

			95% Confidence Interval	
Variable	β	SE	Lower	Upper
Intercept	-2.86	0.36	-3.55	-2.18
Habitat [a]				
Cultivated	2.38	0.47	1.46	3.33
Degraded	-0.26	0.74	-1.76	1.15
Urban built-up	0.06	0.88	-1.58	1.73
Wetland	5.86	0.47	4.94	6.78
Rainfall [b]				
Wet	1.96	0.42	1.15	2.78
Site [c]				
STR	0.45	0.44	-0.41	1.33
Habitat x Rainfall	-0.83	0.57	-1.93	0.28
Cultivated x wet	-1.62	0.80	-3.22	-0.08
Degraded x wet	-2.96	0.81	-4.57	-1.41
Urban built-up x wet	-2.36	0.58	-3.48	-1.22
Wetland x wet				
Habitat x Site				
Cultivated x STR	0.14	0.58	-0.99	1.29
Degraded x STR	0.19	0.81	-1.41	1.79
Urban built-up x STR	0.41	0.93	-1.43	2.19
Wetland x STR	-1.59	0.59	-2.75	-0.42

[a] Reference = natural
[b] Reference = dry
[c] Reference = BAR

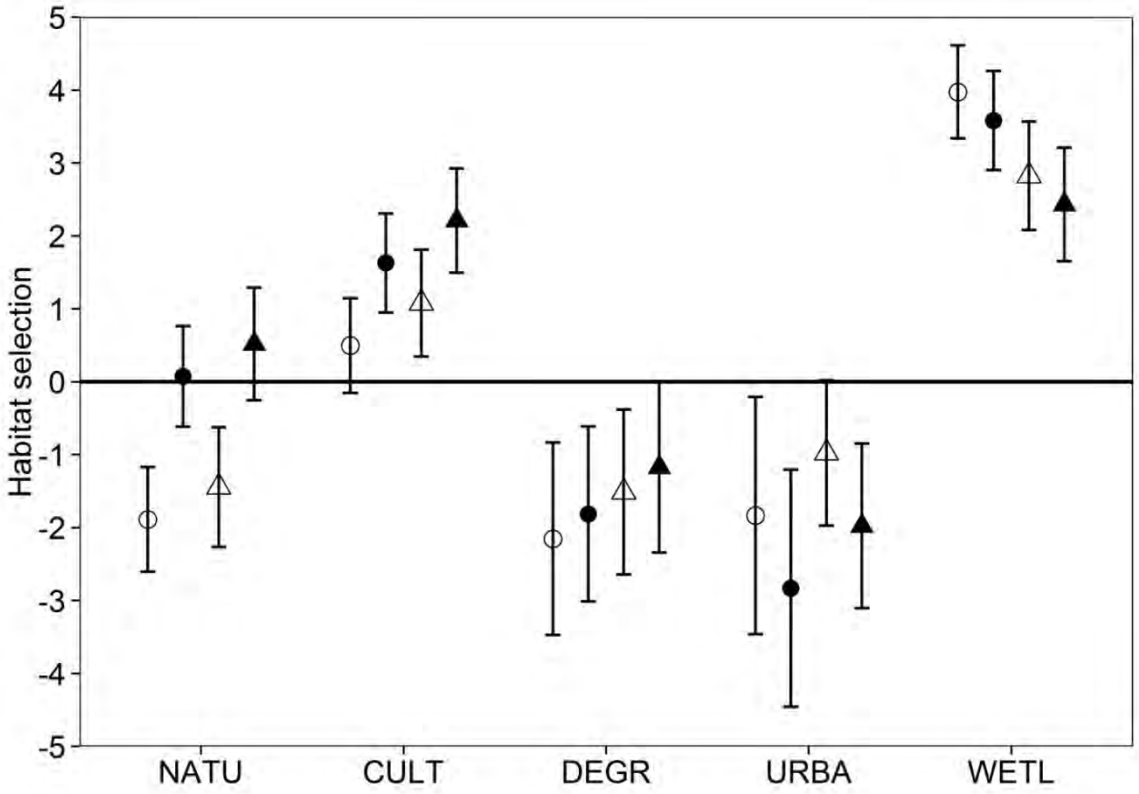


Figure 3.5 Habitat selection of five habitat types by Egyptian Geese at the home range scale for each rainfall season and site (Open circles, Barberspan dry season; filled circles, Barberspan wet season; open triangles, Strandfontein dry season; filled triangles, Strandfontein wet season). The horizontal line indicates a level of use which is proportional to availability. Values above the line indicate selection while those below indicate avoidance. Bars represent 95% confidence intervals of parameter estimates. NATU, natural; CULT, cultivated; DEGR, degraded; URBA, urban-built up; WETL, wetlands. See Appendix 1 for classification of habitat types.

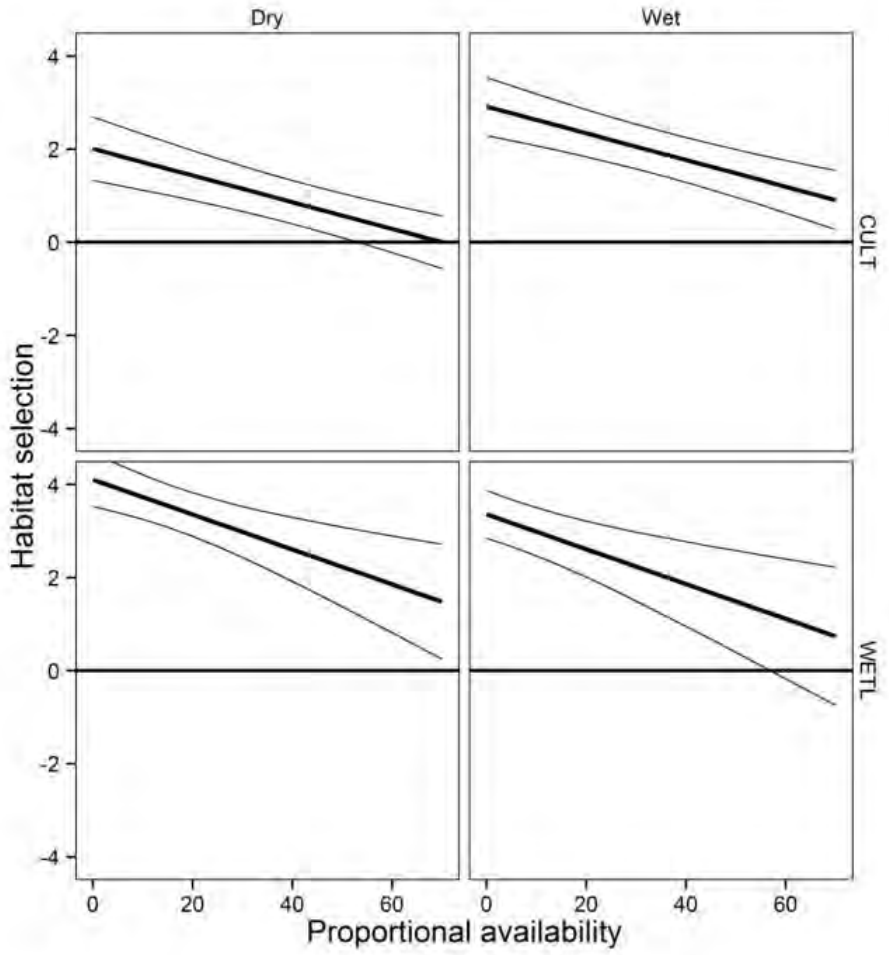


Figure 3.6 Relationship between proportional availability and habitat selection (indicating a functional response) of Egyptian Geese for cultivated (CULT) and wetland (WETL) habitat in each rainfall season. The horizontal line indicates a level of use which proportional to availability. Values above the line indicate selection while those below indicate avoidance. Thin regression lines represent 95% confidence intervals of parameter estimates.

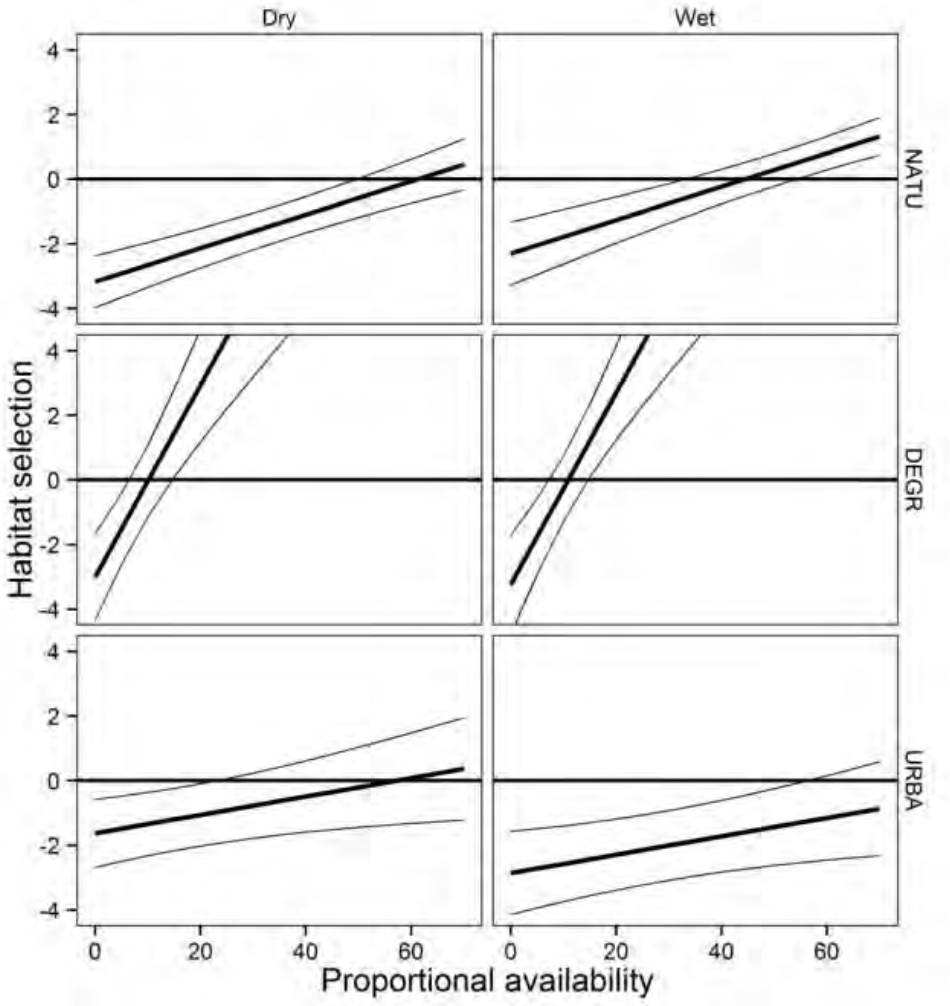


Figure 3.7 Relationship between proportional availability and habitat selection (indicating a functional response) of Egyptian Geese for natural (NATU), degraded (DEGR) and urban-built up (URBA) habitat in each rainfall season. The horizontal line indicates a level of use which is proportional to availability. Values above the line indicate selection while those below indicate avoidance. Thin regression lines represent 95% confidence intervals of parameter estimates.

3.5 Discussion

Habitat selection patterns for Egyptian Geese were primarily driven by external factors, in that variation occurred between rainfall seasons and study sites (Fig. 3.5). I found little statistical support for including life stage in the habitat selection model (Table 3.2), which suggests that the effect of internal factors (Nathan et al. 2008) on selection patterns was weak. This implies that Egyptian Geese make habitat choices in response to changes in underlying landscape resources. Unsurprisingly, Geese showed marked selection for wetlands, which provide habitat for breeding, safety and comfort activities such as preening and loafing, throughout the year. Nevertheless, there were site and seasonal differences in the magnitude of selection for wetlands. As terrestrial productivity decreased in the dry season, selection for aquatic resources increased, with higher levels of selection occurring in Geese from Barberspan. Egyptian Geese are able to dabble in shallow water (Milstein 1993) and it is possible that as the quantity of terrestrial grasses decreases, geese become more reliant on aquatic plant growth to fulfil their energy requirements.

Although overall selection was not significant for urban habitats, there was an increase in their use during the dry season, especially for geese from the Strandfontein population. Many parks, fields, and lawns are irrigated year-round, providing fresh grazing. The observed pattern suggests that in addition to aquatic forage, geese may be supplementing their diet with grazing in urban areas. Geese are often associated with golf courses, and in some cases are considered pests (Little and Sutton 2013). Golf courses are usually located within urban areas, and I expected use of urban habitats to be higher than that observed in my study. However this pattern of low use is most likely due to how golf courses were classified in the latest version of the NLC map. According to the 2000 NLC classification (Appendix 1), golf courses fall within the planted grassland category, which was incorporated into the cultivated habitat category for 2009 NLC map.

Patterns in selection of cultivated land were consistent with the hypothesis that range expansion in Egyptian Geese is due their association with croplands (Hockey et al. 2005, Okes et al. 2008). At both study sites, selection for cultivated land was highest in the wet season, which correlates with the growing season and high levels of productivity in croplands. Selection was more pronounced in Strandfontein Geese through both seasons. Numbers of Geese in Western Cape croplands peak between May and August (wet season), where birds feed primarily on barley and wheat (Mangnall and Crowe 2001, 2002). Egyptian

Geese feed on surface seeds in May, and switch to feeding on growing plants from June onwards. Although they use croplands to a lesser extent in the dry summer months, food is still available and used in the form of stubble and ripe crops stored in windrows (Mangnall and Crowe 2002). Maize is the dominant crop surrounding Barberspan and there is evidence that Geese use this as a food source (Milstein 1993). However, detailed research on the relationship between Egyptian Goose abundance and the dynamics of crop cycles has not been carried out in that region. In the dry winter months, selection of cultivated land was positive but not significant. This suggests that in contrast to Western Cape farms, food resources in the dry season in summer rainfall croplands may not be adequate to sustain the energetic needs of geese. Patterns of selection for natural habitat mirrored those of cultivated land, although at a lower level of overall selection. This again suggests that landscape productivity was affecting use of natural habitats, with geese preferring natural habitat during the wet season at both sites.

In all habitats, the direction of selection was the same in each of the two sites (i.e. if selection for a habitat was higher in a certain season then it was true for Geese from both Strandfontein and Barberspan; Fig. 3.5). This pattern, combined with the finding that the effect of individuals contributed only a fraction of explained variance in the full model, suggests that Egyptian Geese are making similar decisions about habitat use at the home range scale, even when occupying vastly different landscapes. This is surprising, given that other studies have shown that waterfowl occupying patchy landscapes exhibit a high degree of individual variability in movement patterns in response to similar landscape conditions (Roshier et al. 2008a, Oppel et al. 2009). It has been proposed that this variability could occur as a result of differing behavioural strategies which are in turn influenced by several factors, including spatial memory, energy reserve dynamics and competition (Zollner and Lima 2005, Doerr and Doerr 2005a). These studies did not however examine habitat selection directly with RSFs. Cumming, Gaidet & Ndlovu (2012) showed that Egyptian Geese displayed significantly different movements patterns between Barberspan and Strandfontein, which is also evident in Fig. 3.1 & 3.2. This suggests that there is a discord in findings between studies examining only properties of movement trajectories and studies, such as this one, considering only point patterns. Integration of both methods is therefore a necessary analytical step towards a more comprehensive understanding of movements.

Functional responses in habitat selection are expected to occur when animals face trade-offs that affect the amount of time spent in each habitat (Mysterud and Ims 1998). Here

I examined trade-offs between minimising the risk of predation and high quality forage. A negative functional response is expected to occur when the use of one habitat happens at the expense of another resource (Mabille et al. 2012). In both seasons, Geese exhibited a negative functional response in selection for wetland and cultivated habitat (Fig. 3.6), meaning that as the relative proportion of these habitats within the home range decreased, selection for that habitat increased. The strength of response in cultivated habitat was stronger in the wet season, while that of wetlands was similar through both seasons. The inverse relationship (i.e. a positive functional response) was observed in natural, degraded and urban habitats, where selection for these habitats increased with their proportional availability. A negative functional response for both cultivated and wetland habitat was a surprising result. If Egyptian Geese face a trade-off between predation risk and high quality food, one would expect a negative functional response in the use of the habitat that provided best access to these limiting factors, not in both habitats. When faced with predation risk, herbivores are expected to use habitats where they feel safer, but where forage quality may be poorer (Benhaiem et al. 2008, Herfindal et al. 2009). Wetlands can certainly be regarded as safer habitats because they provide vegetation cover which reduces risk of predation while geese also benefit from vigilance and alert behaviour of other wetland birds. When compared to the nutritional quality of cereal crops in cultivated land, wetlands provide access to poorer quality forage. Indeed, predation risk seems to play a factor in foraging decisions as Egyptian Geese have been shown to abandon cultivated fields when vegetation height exceeds 25 cm, presumably because their field of view is impaired, reducing their ability to detect predators (Mangnall and Crowe 2002). An additional risk when foraging on cultivated fields arises from farmers who employ wingshooting to kill or scare Egyptian geese to reduce the extent of crop damage the birds can cause (Mangnall and Crowe 2001). It has been found that risk of disturbance by humans can have similar affects on fitness as those resulting from 'natural' predation risk, and in anthropogenically modified landscapes, animals face foraging-disturbance trade-offs (Frid and Dill 2002). For example, Gill, Sutherland & Watkinson (1996) found that Pink-footed Geese, *Anser brachyrhynchus,* decreased their exploitation of cultivated land as a function of increasing distance from roads which are associated with disturbance. My results therefore suggest that both safety from predators and high quality food resources could possibly be limiting factors at the home range scale, however based on the methods applied here it is difficult to rank the relative importance of each.

Identifying the resources involved in trade-offs can provide information on limiting factors and how they interact at specific scales. An important point is that limiting factors and habitat selection differ according to the scale of enquiry (Boyce et al. 2003, Boyce 2006). It has been proposed that the factors that have the greatest impact on animal fitness should operate at the largest scales (Dussault *et al.* 2005), and it is preferable to consider multiple scales when analysing habitat selection. Habitat selection at the landscape scale considers how animals select their home ranges within a broader geographic area (2nd order selection, Johnson 1980). Measuring availability of habitat resources at broader extents is different for animals such as ungulates, whose movements may be restricted to islands, conservation areas, or reserves. The extent of the study 'landscape' in many studies is significantly smaller than that of this study. Assessing selection among highly mobile and far-ranging waterfowl at broad scales therefore provides a significant challenge. The lack of geographical barriers in southern Africa (Hockey 2000), coupled with the high movement capacity of Egyptian geese (Fig. 3.1), makes it difficult to objectively quantify the habitat that is actually available to individuals. Without knowing the range of resources available to an animal, implementing RSFs under the use-availability design is not possible. Egyptian Geese could theoretically move far in a very short space of time, which is evident from an individual (PTT 77127) which flew over 1000km in several hours. This restricts the inferences that I am able to make about limiting factors at any scale larger than the home range, and current methods using the RSF framework have not identified ways to address this. Although the analysis was based on a relatively small sample of 10 individuals, the results nonetheless show for the first time that habitat use by Egyptian Geese is strongly influenced by resource availability at the home range scale.

This study provides the first application of mixed effects RSFs methods to assess habitat selection of waterfowl living in arid landscapes. I have shown that in addition to wetlands, cultivated land provides an essential habitat resource for Egyptian Geese, as functional responses for both of these habitats were evident. Selection choices of individuals from both study populations were very similar, suggesting a level of synchrony in how Egyptian Geese use habitat patches at the home range scale. Egyptian Geese displayed a functional response in habitat selection for contrasting habitats of wetlands and cultivated lands, however no clear signal emerged as to whether forage or predation risk were the most limiting factor at the home range scale.

To respond to unpredictable changes in resource distributions, nomadic animals must to some degree employ flexible strategies of habitat use. The strength of trade-offs between forage quality and predation risk should therefore change between seasons in response to animals adapting to landscape conditions. My results did not identify significant differences in trade-offs across seasons and sites, but the strength of the effect of predation might only become apparent under extreme weather conditions, where animals might give higher priority to foraging over the risk of predation (Cresswell 1994, 2008). The landscapes that Egyptian Geese moved across did not experience any severe droughts during the study period, meaning that they were not under heavy pressure to spend extended periods in irrigated agricultural habitats at the sacrifice of time spent in safer wetland habitats. Understanding fitness consequences and population dynamics of nomadic animals therefore requires studying functional responses over extended temporal scales to detect changes in trade-offs and habitat use through a range of ecological conditions. Doing so will provide insights into how the relevant trade-offs shape animal movements at broad extents and will ultimately increase our understanding of the ecology and conservation of nomadic animal populations living in dynamic landscapes.

3.6 Appendix

Appendix 1 Details of how the habitats in the 2009 National Landcover (NLC) map of South Africa were derived from the 2000 classification. Habitat available to Egyptian Geese in the study was measured according to the 2009 classification.

ID	NLC 2009	ID	NLC 2000
1	Natural	1	Forest (indigenous)
1	Natural	2	Woodland
1	Natural	3	Thicket, Bushland, Bush Clumps & High Fynbos
1	Natural	4	Shrubland & Low Fynbos
1	Natural	5	Herbland
1	Natural	6	Natural Grassland
2	Cultivation	7	Planted Grassland
6	Plantations	8	Forest Plantations (Eucalyptus spp)
6	Plantations	9	Forest Plantations (Pine spp)
6	Plantations	10	Forest Plantations (Acacia spp)
6	Plantations	11	Forest Plantations (other / mixed spp)
6	Plantations	12	Forest Plantations (clearfelled)
5	Waterbodies	13	Waterbodies
5	Waterbodies	14	Wetlands
1	Natural	15	Bare Rock & Soil (natural)
1	Natural	16	Bare Rock & Soil (erosion : dongas / gullies)
1	Natural	17	Bare Rock & Soil (erosion : sheet)
3	Degraded	18	Degraded Forest and Woodland
3	Degraded	19	Degraded Thicket, Bushland, etc
3	Degraded	21	Degraded Shrubland & Low Fynbos
3	Degraded	22	Degraded Natural Grassland
2	Cultivation	23	Cultivated, permanent, commercial, irrigated

2	Cultivation	24	Cultivated, permanent, commercial, dryland
2	Cultivation	25	Cultivated, permanent, commercial, sugarcane
2	Cultivation	26	Cultivated, temporary, commercial, irrigated
2	Cultivation	27	Cultivated, temporary, commercial, dryland
2	Cultivation	28	Cultivated, temporary, subsistance, dryland
2	Cultivation	29	Cultivated, temporary, subsistance, irrigated
4	Urban Built-up	30	Urban / Built-up residential
4	Urban Built-up	31	Urban / Builtup : rural cluster
4	Urban Built-up	32	Urban / Built-up : residential, formal suburbs
4	Urban Built-up	33	Urban / Built-up : residential, flatland
4	Urban Built-up	34	Urban / Built-up : residential, mixed
4	Urban Built-up	35	Urban / Built-up : residential, hostels
4	Urban Built-up	36	Urban / Built-up : residential, formal township
4	Urban Built-up	37	Urban / Built-up : residential, informal township
4	Urban Built-up	38	Urban / Built-up : residential, informal squetter camp
4	Urban Built-up	39	Urban / Built-up : smallholdings, woodland
4	Urban Built-up	40	Urban / Built-up : smallholdings, thicket, bushland
4	Urban Built-up	41	Urban / Built-up : smallholdings, shrubland
4	Urban Built-up	42	Urban / Built-up : smallholdings, grassland
4	Urban Built-up	43	Urban / Built-up : commercial - mercantile
4	Urban Built-up	44	Urban / Built-up : commercial - education, health, IT
4	Urban Built-up	45	Urban / Built-up : industrial / transport : heavy
4	Urban Built-up	46	Urban / Built-up : industrial / transport : light
7	Mines	47	Mines & Quarries (underground / subsurface mining)
7	Mines	48	Mines & Quarries (surface-based mining)
7	Mines	49	Mines & Quarries (mine tailings, waste dumps)

4 EXPLORING THE ENVIRONMENTAL DRIVERS OF WATERFOWL MOVEMENT IN ARID LANDSCAPES USING FIRST-PASSAGE TIME ANALYSIS

4.1 Abstract

The movement patterns of many southern African waterfowl are typified by nomadism, which is thought to be a response to unpredictable changes in resource distributions. Nomadism and the related movement choices that waterfowl make in arid environments are, however, poorly understood. Tracking multiple individuals across wide spatiotemporal gradients offers one approach to elucidating the cues and mechanisms underpinning movement decisions. I used first-passage time (FPT) to analyse high spatial and temporal resolution telemetry data for Red-billed Teal and Egyptian Geese across a 1500 km geographical gradient between 2008 and 2014. I tested the importance of several environmental variables in structuring movement patterns, focusing on two competing hypotheses: (1) whether movements are driven by resource conditions during the current period of habitat occupation (reactive movement hypothesis), or (2) whether movements are structured by shifts in the magnitude and direction of environmental variables at locations prior to occupation (prescient movement hypothesis). An increase in rainfall at a 32 day lag (i.e., prior to wetland occupancy), along with tagging site, were significant predictors of FPT in both waterfowl species. There was a positive relationship between NDVI and FPT for Egyptian Geese during this 32 day period; the relationship was negative for Red-billed Teal. Consistent with findings for migratory grazing geese, Egyptian Geese prioritised food quality over food biomass. Red-billed Teal showed few immediate responses to wetland filling, contrary to what one would predict for a dabbling duck, suggesting high dietary flexibility. My results were consistent with the prescient movement hypothesis. Using FPT analysis I showed that the proximate drivers of southern African waterfowl movement are the dynamics of rainfall and primary productivity. Waterfowl appeared to be able to perceive and respond to temporal shifts in resource conditions prior to habitat patch occupation. This in turn suggests that their movements in semi-arid landscapes may be underpinned by intimate

knowledge of the local environment; waterfowl pursue a complex behavioural strategy, locating suitable habitat patches proactively, rather than acting as passive respondents.

4.2 Introduction

Processes that drive movement occur on a wide range of spatiotemporal scales and are important for the structure and dynamics of populations, communities and ecosystems (Turchin 1998, Hanski 1999). In order to adequately link movement patterns and changes in landscape conditions it is necessary to track multiple individuals across broad geographic and seasonal gradients, while simultaneously accurately quantifying the dynamics of landscape resources of interest (van Moorter et al. 2013). The development of lightweight tracking devices with the ability to record high resolution movement data, coupled with broad scale remote sensing data has in many cases made this possible (Boettiger et al. 2011, Avgar et al. 2013, Trierweiler et al. 2013). However, an important challenge lies in detecting phases of movement within the complete path, as well as revealing the environmental factors that drive the emergence and persistence of these phases (Nathan et al. 2008).

Under certain circumstances theory suggests that animals should move slowly and tortuously through habitats containing high quality resources (Fauchald and Tveraa 2006) – a behaviour analogous to Area-Restricted Search (ARS; (Kareiva and Odell 1987)). Patches in which movement is tortuous should be profitable habitats which provide adequate resources that increase fitness through energy acquisition, reproduction and survival. Animals should avoid areas that have negative fitness consequences by moving more quickly and linearly through them. Identifying landscape characteristics in which movements are clustered can provide insight into the factors that shape an animal's movement through a landscape. It is important to note that these movement patterns can be confounded by several factors which may obscure the relationship between environmental resources and habitat use – including the high levels of individual variation in animal movements; competition; predation; social factors and life-stage requirements.

Resources in most ecosystems are heterogeneously distributed across space and through time (Johnson et al. 1992). They are organised within a scale-dependant hierarchy, with aggregations (patches) at smaller scales nesting into those at larger scales (Wiens 1976, Levin 1992). The density and dynamics of available resources therefore depend on the scale(s) at which an animal interacts with the landscape (Wiens and Milne 1989). To maximise fitness, mobile animals should be able to alter their behaviour to exploit resources

at different scales (Fauchald and Tveraa 2006). Animal movement is a potentially vital mechanism for dealing with heterogeneous landscapes and movement patterns should therefore provide evidence for spatial responses (McIntire and Fajardo 2009).

The presence of water is an essential habitat resource for all waterfowl. Wetlands in semi-arid landscapes are dynamic entities and are usually in a state of flux. The landscape that southern African waterbirds inhabit is generally arid, with unpredictable timing and duration of rainfall events (Tyson and Preston-Whyte 2000). The dynamics of filling and drying cycles are primarily driven by the stochastic nature of rainfall events. In southern Africa dry periods are common and can last years, but these can be followed by unpredictable periods of above average rainfall (Siegfried 1970). This creates a spatially and temporally variable mosaic of ephemeral wetlands. Many waterbirds occurring in such areas have adapted to this variability by employing nomadic movements during parts of the year (Oatley and Prys-Jones 1986, Underhill et al. 1999, Roshier et al. 2006). Egyptian Geese *Alopochen aegyptiaca* and Red-billed Teal *Anas erythrorhyncha* are two species of southern African waterfowl that adopt widespread nomadic movements (Hockey et al. 2005). This makes them ideal study species for investigating ARS behaviour in response to environmental heterogeneity.

If waterfowl perform broad scale movements and adopt ARS behaviour opportunistically when suitable resources are encountered, then variation in first-passage time should be best explained by resource conditions in the period during which waterfowl occupy a given area – termed here as the "reactive movement (RM)" hypothesis. This would suggest that movement decisions are a response to current local and immediate environmental conditions. This hypothesis implies the following two predictions: RM_1) If forage availability is an important environmental driver of movements, FPT would be positively correlated with local food biomass, measured by the normalised difference vegetation index (NDVI; (Pettorelli et al. 2005)). Egyptian Geese are primarily grazers and thus are reliant on vegetation which may surround wetlands, while Red-Billed Teal are dabbling ducks and so rely on food resources located within the water column. I would thus expect the effect of vegetation greenness (NDVI) to be stronger for geese than for teal. RM_2) Wetlands are a primary abiotic resource for waterfowl and provide habitats for foraging, roosting, safety from predators, and moult sites. If the extent of a wetland is an important environmental driver of movements, FPT would be positively correlated with either rainfall or wetland area or a combination of both. Many ephemeral wetlands in southern Africa are shallow rain-fed depressions in which

inundation, and hence wetland area, is closely tied to local precipitation events. However, an increase in wetland area is not necessarily associated with higher local rainfall. For example, floodplains can inundate following rainfall events in more distant regions of the catchment basin.

Alternatively, waterfowl may be able to structure their movements in response to changes in the magnitude and direction of resources states leading up to habitat patch occupation. There are a number of potential mechanisms that may drive this behaviour. For instance, well developed spatial memory of the landscape coupled with ability to incorporate information about local weather conditions could allow waterfowl to make movement decisions which are distinctly different to those described in the RM hypothesis. Under this hypothesis, FPT would be best explained by shifts in the magnitude and direction of resource states between the current time of occupation and a lag period prior to bird arrival - here termed the "prescient movement (PM)" hypothesis. I investigated the hypothesis with both 16 and 32 day lag periods. A positive increase in NDVI between two time periods, which reflects changes in vegetative growth, indicates an increase in food quality (Doiron et al. 2013). It has been found that younger plants have higher nutritional quality (higher nitrogen concentration) and lower levels of secondary plant chemicals. Following the Green Wave Hypothesis (GWH) it has been demonstrated that northern hemisphere geese do not select habitats with the highest biomass, but instead time their migration to take advantage of successive peaks of plant nutrition and digestibility (van der Graaf et al. 2006, Shariatinajafabadi et al. 2014). My second hypothesis implies the following two predictions: PM_1) If waterfowl movements are a response to food quality, I would expect FPT to be higher in areas that experienced a positive change in NDVI in the 16 or 32 days prior to occupation of a patch. I would expect this effect to be more important for geese, which are grazers, than for teal, which are traditionally thought to be more reliant on invertebrate and macrophyte food resources. If support for the PM hypothesis emerged I also expected that (PM_2) the first-passage time of Red-billed Teal should be longer in areas that experienced positive changes in wetland cover and/or rainfall prior to bird arrival. For Egyptian Geese I also predicted a positive correlation between FPT and increases in rainfall and wetland area, but I expected this response to be more prominent at the 32 day lag period at which water levels start to recede and vegetation starts to grow on previously submerged shorelines.

These predictions require some additional explanation. Wetlands are dynamic entities and in many cases are either filling or drying down. These two states represent different

opportunities for Egyptian Geese and Red-billed Teal, and a successional response by waterbirds to rainfall events and wetland filling has been demonstrated in arid zone systems (Kingsford et al. 2010, Cumming et al. 2012b). In Australia, Kingsford et al. (2010) found that dabbling ducks arrive first to take advantage of the boom period, when nutrients are mobilised and dormant invertebrates emerge and reproduce. Grazing birds, conversely, have a lagged response to rainfall events and may arrive as wetlands start to dry down, utilizing terrestrial plants that colonize the drying shorelines (Kingsford et al. 2010). Studies in southern Africa have recorded Red-billed Teal arriving at inundated wetlands within days of rainfall events, with numbers peaking after a couple of weeks (Simmons et al. 1999, Herrmann et al. 2004). Large variation in response time appears to exist (e.g., Red-billed Teal abundance peaked 4 months following the inundation of a large river system in Namibia, (Cumming et al. 2012b)).

I addressed the interaction between external factors, characterised by landscape attributes, and the navigation capacity of two species of southern African waterfowl. Navigation capacity describes the ability of organisms to decide when and where to move. Effective navigation requires the ability to detect and respond to the spatial and temporal dynamics of underlying environmental conditions (Nathan et al. 2008). I first used FPT analysis to determine the scale of movement of waterfowl over yearly temporal scales across a 1500 km geographical gradient. I then explored the spatiotemporal dynamics and relative importance of abiotic and biotic variables associated with habitat resources required by waterfowl. I aimed to identify key environmental variables that influence movement behaviour.

4.3 Methods

4.3.1 Sites and study populations

The birds in my study population were captured at three wetland sites in South Africa and one in Zimbabwe: Strandfontein wastewater treatment works; Barberspan Nature Reserve; Jozini Dam and Lake Manyame, respectively (see Figs. 4.1 & 4.2 for capture sites and movement paths of all individuals). See Chapter 2 for site descriptions and capture protocol.

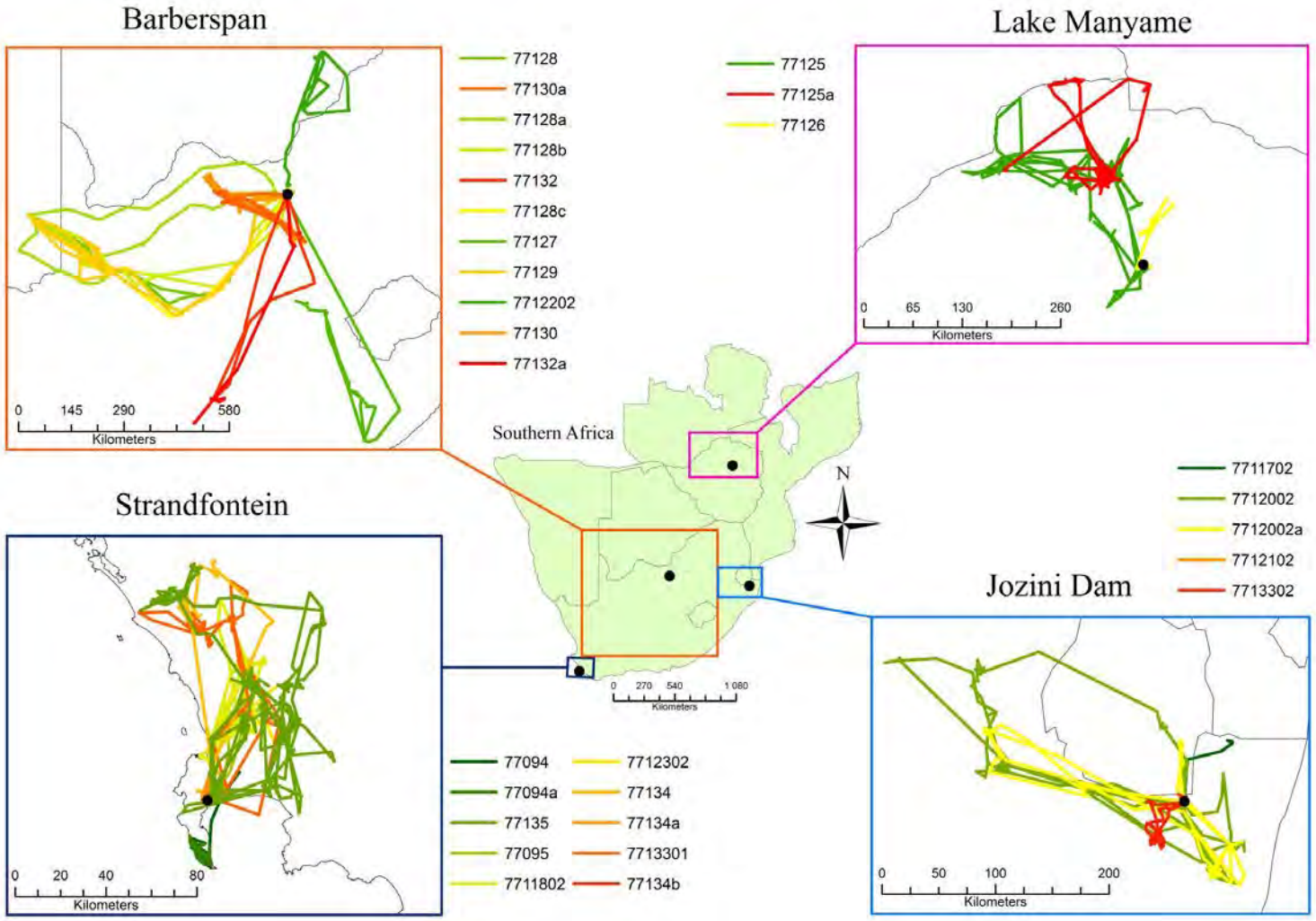


Figure 4.1 Maps showing the movement paths and capture sites of Egyptian Geese in southern Africa over the study period. The legend represents platform transmitter terminal identities of individuals at each site.

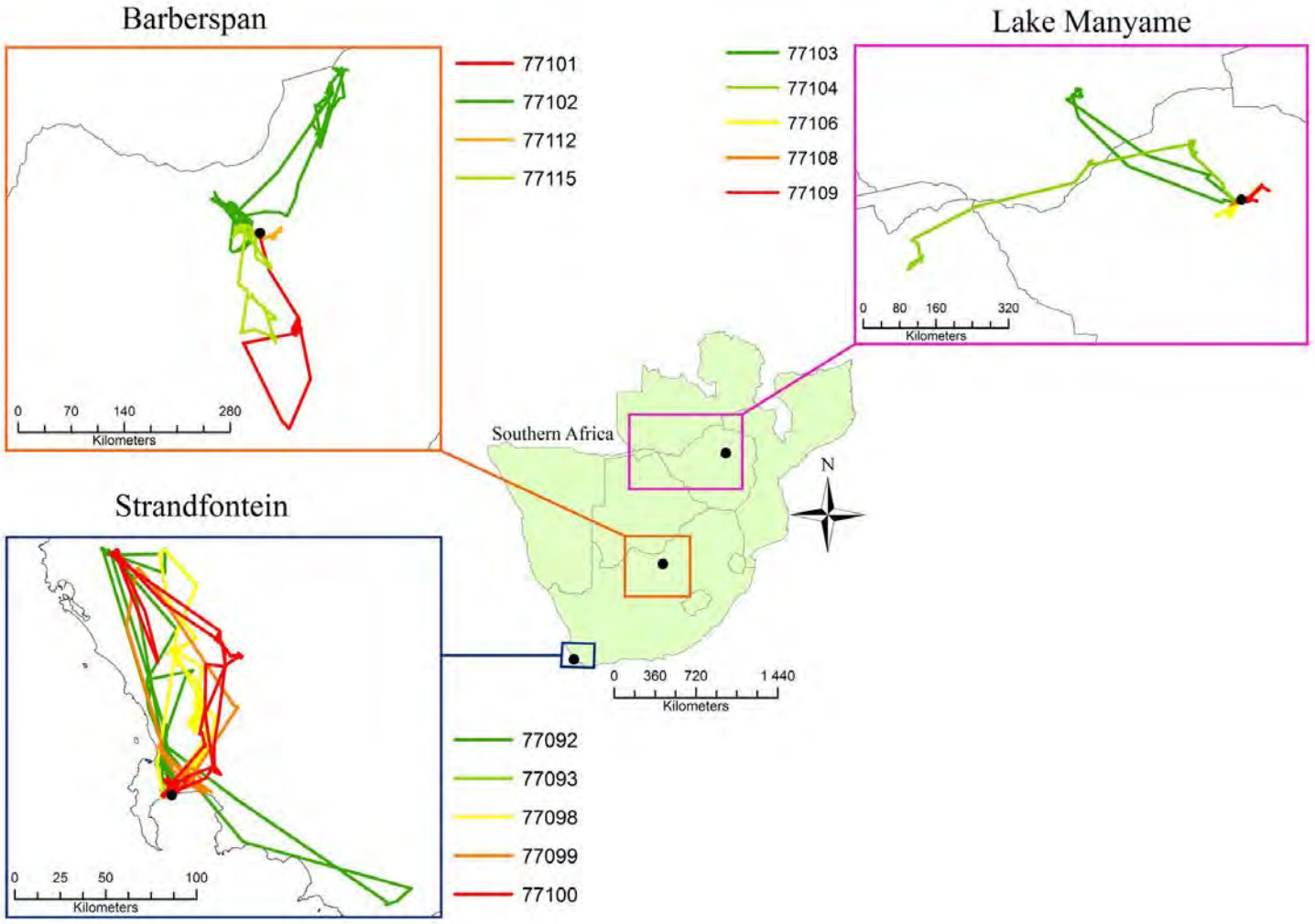


Figure 4.2 Maps showing the movement paths and capture sites of Red-billed Teal in southern Africa over the study period. The legend represents platform transmitter terminal identities of individuals at each site.

4.3.2 Movement data

Birds tracked for less than 90 days were excluded from the analysis. The resulting sample size for Egyptian Geese was n = 19 and Red-billed Teal n = 14. Note that no teal were tagged at Jozini Dam and so data was only available for the three remaining populations. The duration between fixes in the tracks of each bird were inspected and tracks were split if the time between fixes was greater than 1 week (split tracks of each individual are denoted as either *a, b* or *c* dependent on the number of gaps detected). Note that all split tracks had a duration of greater than 90 days.

4.3.3 First-passage time analysis

A graphical example of the analytical steps for the movement path of an individual bird (Red-Billed Teal 77115 from Barberspan) is shown in Fig. 4.3. First-passage time is calculated at each GPS fix along a movement path (Fig. 4.3a) as the time taken to cross a circle of a given radius (Fauchald and Tveraa 2003). The process is repeated over a range of circles with differing radii. The peaks in variance of log transformed FPT at a specific radius (Fig. 4.3b) indicates the scale at which an animal's movements are clustered and hence the spatial scale at which ARS behaviour is occurring (Fauchald and Tveraa 2003). In other words, the peaks correspond to a specific circle radius in which more tortuous and intensive movements are performed. As mean FPT is increases with circle size, I applied a common radius to all bird movement paths of each species, to allow for comparisons of individual bird FPTs. For each species I used the radius at which mean variance of log FPT showed a peak. Following Le Corre et al. (2014), FPT was calculated along an individual's path with a given radius r, ranging from 100 – 10 000 m at 80 m intervals, centred on consecutive locations. The radius r_{max} is the radius at which the variance of log transformed FPT var_{fpt} reaches a maximum. The mean of variance $var_{fpt\ mean}$ was calculated by averaging var_{fpt} of each bird at each radius. The peak in this mean $var_{fpt\ mean}$ was then taken at a population average and used as the common spatial scale for all subsequent analysis.

Once FPT analysis was applied to each individual, plots were created of GPS fixes against FPT (Fig. 4.3c). Lavielle's segmentation method was then applied in order to identify homogenous movement bouts within an individual's movement path using the *lavielle* function in the *adehabitatLT* R package (Calenge 2006, R Core Team 2013). The method aims to detect breakpoints in the movement path by minimizing a penalised contrast function

(Lavielle 2005). Given that a movement path is made up of K segments, the method searches for an optimal number of segments K_{opt} with which to partition the movement path. There should be a clear break in the decrease of the contrast function after K_{opt}, which I identified in two ways. Firstly the break and the corresponding K_{opt}, was visually detected from the plot of the contrast function. Secondly, K_{opt} was automatically detected by choosing the last value of K at which the second derivative of the standardised contrast function is greater than a threshold S. Following the recommendation of Lavielle (2005) S was set to 0.75. These methods were used in conjunction with one another to determine the number of segments for each individual's movement path (Figs. 4.3c & 4.3d).

Segments from each movement path (i.e. paths from all individuals across each site) were extracted and processed in the following way: GPS fixes within segments were used to create utilisation distribution which defined an area and time over which environmental variables could be measured (Fig. 4.3e). Utilisation distributions were calculated with Movement-based Kernel Density Estimator (MKDE) methods (Benhamou and Riotte-Lambert 2012) using the *BRB* function within the *adehabitatHR* R package (Calenge 2006). In order to reduce the effects of autocorrelation inherent in the data, I calculated a mean first-passage time value at the peak radius ($mFPT_{Rmax}$) derived from all GPS fixes contained within the home-range polygon. If the home range was made up of multiple polygons, as is common when using MKDE methods, $mFPT_{Rmax}$ was calculated for each polygon individually. Each polygon was then used as a sampling unit in which $mFPT_{Rmax}$ was the response variable and the set of environmental variables measured in that polygon were the explanatory variables (Fig. 4.3e).

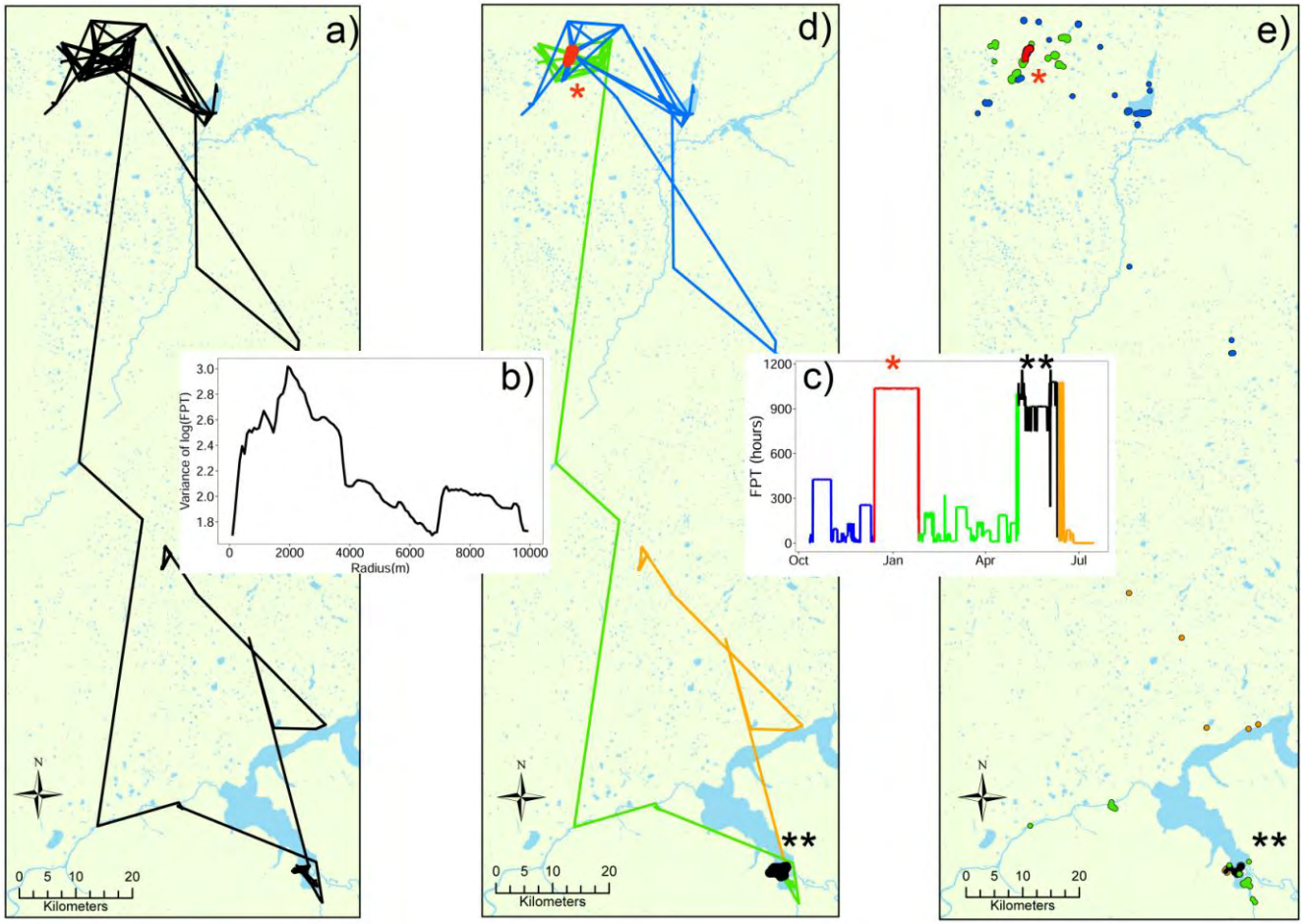


Figure 4.3 Five sequential steps which illustrate the analytical processes carried out on all birds. The movement path in this example was taken from a Red-Billed Teal (77115) tagged in Barberspan. a) The full movement path of the individual. b) The output of the first-passage time (FPT) procedure which identifies the scale at which movements are clustered. The scale corresponds to the radius at which the variance of log(FPT) is at a maximum. c) A graph of the magnitude of FPT at each GPS fix. The five colours each represent a movement segment identified by the Lavielle segmentation process. The red and black segments illustrate areas in which movements are highly clustered and non-linear. d) The initial movement path colour coded according to the corresponding segment from step c. The asterisks indicate the location of the two highly clustered movement segments (red and black). e) The utilisation distributions polygons derived from applying kernel density estimators to movement paths from each segment. Each polygon represents a sampling unit in the statistical analysis where mean FPT and environmental variables were measured.

4.3.4 Environmental data

In order to evaluate the relationship between FPT and environmental conditions, 12 variables were calculated for each home range polygon for each bird. Extraction of environmental variables was performed using Google Earth Engine (https://earthengine.google.com), a cloud platform for the analysis of geospatial data. NDVI, rainfall, water surface coverage (modified normalised difference water index; mNDWI), elevation and temperature were calculated as mean values over the time *t* for which the home range was occupied (Table 4.1). Two extra sets of NDVI, rainfall and mNDWI variables were calculated: 1) the difference between mean at time *t* and *t-16* days and 2) the difference between mean at time *t* and *t-32days*. A positive change in NDVI between time periods would indicate and increase in vegetative growth and hence food quality, while a positive change in mNDWI would indicate an increase in wetland extent. Time lags were chosen to correspond with the minimum temporal resolution of the predictor variables (constrained by the resolution of NDVI which is based on 16 day composites – see Table 4.1 for derivations and sources of data). Dynamic variables were first averaged temporally for the duration of home range occupation, followed by spatial averaging. Geographical location of capture sites was added as a predictor variable to evaluate a study area effect on first-passage times. This included four- and three-level categorical variables for Egyptian Geese and Red-billed Teal respectively. Temperature and elevation were added as fixed effects in some candidate models to assess whether there was an effect of thermal stress on movement behaviour. I developed a set of 36 singular and multi-term candidate models to evaluate my competing hypotheses (Table 4.2).

Table 4.1 Details of environmental variables used as predictors in the analysis of first-passage time (FPT) of two waterfowl species in southern Africa.

		Source	Units	Spatial resolution	Temporal resolution	Earth Engine Layer
NDVI	Normalised difference vegetation index NDVI = (NIR – R)/(NIR + R)	MODIS terra		250m	16-day composite	MODIS/MCD43A4_NDVI
mNDWI	Modified normalised difference water index mNDWI = (G-MIR)/(G+MIR)	MODIS terra		250m	16-day composite	MODIS/MCD43A4
Precip	Rainfall	TRMM	mm/hr	0.25 °	3 hourly	TRMM/3B42
Temp	Land surface temperature	MODIS	K	1km	Daily	MODIS/MYD11A1
Elev	Elevation	NASA	m.a.s.l	0.9km	N/A	CGIAR/SRTM90_V4

Table 4.2 Candidate set of generalised linear mixed models used to investigate the relationship between mean first-passage time (mFPTRmax) and environmental variables of Egyptian Geese and Red-billed Teal. Individual birds (ID) were added as a random effect to all models. See Table 4.1 and text in *Methods* for derivation of environmental predictor variables. RM, reactive movement; PM, prescient movement.

Model		**Model formula**
1	Food quantity	$mFPT_{Rmax} \sim NDVI_t + (1\|ID)$
2	Food quality (16 day)	$mFPT_{Rmax} \sim \Delta NDVI_{t-16} + (1\|ID)$
3	Food quality (32 day)	$mFPT_{Rmax} \sim \Delta NDVI_{t-32} + (1\|ID)$
4	Wetland cover	$mFPT_{Rmax} \sim mNDWI_t + (1\|ID)$
5	Wetland cover change (16 day)	$mFPT_{Rmax} \sim \Delta mNDWI_{t-16} + (1\|ID)$
6	Wetland cover change (32 day)	$mFPT_{Rmax} \sim \Delta mNDWI_{t-32} + (1\|ID)$
7	Precipitation	$mFPT_{Rmax} \sim Precip_t + (1\|ID)$
8	Precipitation (16 day)	$mFPT_{Rmax} \sim \Delta Precip_{t-16} + (1\|ID)$
9	Precipitation (32 day)	$mFPT_{Rmax} \sim \Delta Precip_{t-32} + (1\|ID)$
10	Site	$mFPT_{Rmax} \sim site + (1\|ID)$
11	Temperature & elevation	$mFPT_{Rmax} \sim Temp + Elev + (1\|ID)$

		RM hypothesis: *	
12 (16)		Food quantity, wetland cover & precipitation (+ temperature & elevation, site)	$mFPT_{Rmax} \sim NDVI_t + mNDWI_t + Precip_t + (1\|ID)$
13 (17)		Food quantity & wetland cover (+ temperature & elevation, site)	$mFPT_{Rmax} \sim NDVI_t + mNDWI_t + (1\|ID)$
14 (18)		Food quantity & precipitation (+ temperature & elevation, site)	$mFPT_{Rmax} \sim NDVI_t + Precip_t + (1\|ID)$
15 (19)		Wetland cover & precipitation (+ temperature & elevation, site)	$mFPT_{Rmax} \sim mNDWI_t + Precip_t + (1\|ID)$
		PM hypothesis: **	
20 (24)	16 day	Change in food quality, wetland cover & precipitation (+ site)	$mFPT_{Rmax} \sim \Delta NDVI_{t-16} + \Delta mNDWI_{t-16} + \Delta Precip_{t-16} + (1\|ID)$
21 (25)		Change in food quality & wetland cover (+ site)	$mFPT_{Rmax} \sim \Delta NDVI_{t-16} + \Delta mNDWI_{t-16} + (1\|ID)$
22 (26)		Change in food quality & precipitation (+ site)	$mFPT_{Rmax} \sim \Delta NDVI_{t-16} + \Delta Precip_{t-16} + (1\|ID)$
23 (27)		Change in wetland cover change & precipitation (+ site)	$mFPT_{Rmax} \sim \Delta mNDWI_{t-16} + \Delta Precip_{t-16} + (1\|ID)$
28 (32)	32 day	Change in food quality, wetland cover & precipitation (+ site)	$mFPT_{Rmax} \sim \Delta NDVI_{t-32} + \Delta mNDWI_{t-32} + \Delta Precip_{t-32} + (1\|ID)$
29 (33)		Change in food quality & wetland cover (+ site)	$mFPT_{Rmax} \sim \Delta NDVI_{t-32} + \Delta mNDWI_{t-32} + (1\|ID)$
30 (34)		Change in food quality & precipitation (+ site)	$mFPT_{Rmax} \sim \Delta NDVI_{t-32} + \Delta Precip_{t-32} + (1\|ID)$
31 (35)		Change in wetland cover change & precipitation (+ site)	$mFPT_{Rmax} \sim \Delta mNDWI_{t-32} + \Delta Precip_{t-32} + (1\|ID)$
36		Null	$mFPT_{Rmax} \sim 1 + (1\|ID)$

**Models numbers in parentheses comprise of the same set of environmental predictors with extra addition of site, temp and elevation as a predictor variables.*

***Models numbers in parentheses comprise of the same set of environmental predictors with extra addition of site as a predictor variable.*

4.3.5 Statistical analyses

Generalised linear mixed models were used to model the relationship between $mFPT_{Rmax}$ and environmental variables using the *lmer* function from the R package *lme4* (Bates et al. 2014). Data were first screened for normality, and outliers were removed. $mFPT_{Rmax}$ was log-transformed prior to inclusion into candidate models. Individual birds were added as random effect to allow for estimation of population level regression coefficients while accounting for variation between individuals. All predictor variables were scaled before inclusion into the models. This allowed for standardisation of parameter estimates and comparison of their magnitudes. Spatial auto-correlation in the residuals of the chosen models was examined in two ways. First, I visually examined spatial plots of the magnitude and signs of residuals; and second, I used semi-variograms to quantify variance as a function of distance between points (*bubble* and *variogram* function from *gstat* R package, (Pebesma 2004)). Model selection followed evaluation of candidate models from AIC criteria (Burnham and Anderson 2002). Variance inflation factors were used to test for the presence of collinearity amongst predictor variables. R^2_{GLMM} was used as a measure of overall fit for the selected models (Nakagawa and Schielzeth 2013).

4.4 Results

After calculating var_{fpt} for each individual against radius (Figs. 4.4 & 4.5), the mean radius r_{max} for Egyptian Geese and Red-billed Teal were identified as 2180 and 2420m. The results of the subsequent FPT analysis showed that the number of movement segments ranged from 2 – 7 (mean 4). The number of utilisation distribution polygons derived from the segments ranged from 4 – 120 (mean 38.2). The area of those utilisation distribution polygons ranged from 1.5 – 3.4km^2 (mean 2.3km^2). The number of days spent in a specific utilisation distribution polygon ranged from 4 – 47 (mean 15). See Table 4.3 for the above values of each individual.

Table 4.3 Details of individual GPS-tagged Egyptian Geese (EG) and Red-billed Teal (RBT). PTT, transmitter identity; BAR, Barberspan; STR, Strandfontein; MAN, Lake Manyame; JOZ, Jozini Dam. Start and end date refers to the time period of tracking data used in the study (ND is the total tracking duration in days). Total fixes (TF) are the number of relocations recorded over the study period, while mean fixes per day (FD) are the total number of relocations divided by the number of days the transmitter was active. The remaining columns contain data from the results of the FPT analysis. NS, number of movement segments per track; UDs, number of utilisation distributions derived from all segments; UDA, mean (± sd) area of utilisation distributions; UDD, mean (± sd) number of days spent in each utilisation distribution polygon.

PTT	Spp	Site	Start	End	ND	TF	FD	NS	UDs	UDA (km^2)	UDD (days)
77092	RBT	STR	3/12/2008	3/26/2009	379	1804	4.8	5	31	2.24 ± 2.42	15.8 ± 23
77093	RBT	STR	3/12/2008	9/7/2008	179	993	5.5	3	12	1.95 ± 1.24	22.1 ± 20.7
77098	RBT	STR	3/14/2008	11/24/2009	620	3550	5.7	5	44	2.26 ± 2.18	20.6 ± 30.8
77099	RBT	STR	3/14/2008	5/15/2009	427	1859	4.4	4	23	3.41 ± 3.27	20.8 ± 25.2
77100	RBT	STR	3/14/2008	4/16/2009	398	2046	5.1	6	42	1.95 ± 1.32	14.5 ± 16.9
77101	RBT	BAR	4/9/2008	9/28/2008	172	740	4.3	3	11	3.42 ± 2.19	22.2 ± 22.6
77102	RBT	BAR	4/10/2008	4/20/2010	740	4155	5.6	4	82	1.54 ± 0.98	13.5 ± 24
77103	RBT	MAN	5/5/2008	8/24/2008	111	610	5.5	3	33	2.57 ± 2.73	6 ± 7.6
77104	RBT	MAN	5/5/2008	1/25/2009	265	1431	5.4	3	43	1.79 ± 1.74	10.3 ± 21.3
77106	RBT	MAN	5/6/2008	7/25/2009	445	2587	5.8	7	34	2.3 ± 2.09	19.4 ± 25.2
77108	RBT	MAN	5/6/2008	8/29/2008	115	644	5.6	4	22	2.67 ± 3.1	10.5 ± 11.9
77109	RBT	MAN	5/7/2008	12/24/2008	231	1307	5.7	4	37	1.88 ± 1.12	12.3 ± 23.2
77112	RBT	BAR	6/7/2008	5/15/2009	342	1843	5.4	3	23	2.15 ± 2.49	21.8 ± 43.6
77115	RBT	BAR	10/11/2008	7/15/2009	277	1429	5.2	4	20	2.16 ± 1.37	11.6 ± 15
77094	EG	STR	1/12/2008	5/9/2008	118	1218	10.3	4	15	1.99 ± 1.14	12.1 ± 9.6
77094a	EG	STR	8/20/2008	5/1/2009	254	2686	10.6	3	9	2.59 ± 2.29	21.2 ± 34.3
77095	EG	STR	1/12/2008	1/3/2009	357	3397	9.5	5	32	2.29 ± 1.93	15.5 ± 22.3
7711702	EG	JOZ	5/4/2012	9/20/2012	139	1669	12.0	5	13	2.25 ± 1.24	13.3 ± 13.9
7711802	EG	STR	1/17/2009	10/11/2010	632	6453	10.2	5	58	2.56 ± 2.93	18.1 ± 31.3
7712002	EG	JOZ	5/4/2012	5/24/2013	385	4317	11.2	2	86	3.12 ± 3.06	11.5 ± 17.7
7712002a	EG	JOZ	6/9/2013	1/31/2014	236	2592	11.0	3	43	1.93 ± 1.6	10.9 ± 15.9

7712102	EG	JOZ	5/5/2012	9/3/2012	121	1309	10.8	3	4	2.21 ± 1.19	30.5 ± 19.8
7712202	EG	BAR	10/23/2008	5/30/2009	219	2123	9.7	5	37	1.87 ± 1.7	8.5 ± 13.4
7712302	EG	STR	12/5/2008	6/2/2009	179	1756	9.8	4	7	2.53 ± 1.26	23.9 ± 30.7
77125	EG	MAN	5/7/2008	2/21/2010	655	6965	10.6	5	120	2.29 ± 2.98	11.6 ± 24.1
77125a	EG	MAN	4/17/2010	5/31/2011	409	3689	9.0	3	60	2.68 ± 2.76	15.6 ± 21.4
77126	EG	MAN	5/7/2008	12/26/2008	233	2682	11.5	5	29	2.33 ± 2.86	12.6 ± 16.5
77127	EG	BAR	6/7/2008	5/10/2010	702	6351	9.0	6	54	2.7 ± 3.32	17.3 ± 26.9
77128	EG	BAR	6/22/2008	6/6/2009	349	3551	10.2	3	31	1.81 ± 1.9	10.4 ± 25.4
77128a	EG	BAR	8/15/2009	5/25/2010	283	2551	9.0	3	64	1.81 ± 1.9	6.5 ± 14.3
77128b	EG	BAR	9/25/2010	5/6/2011	223	1998	9.0	3	28	1.67 ± 0.96	5.7 ± 12.1
77128c	EG	BAR	7/31/2011	12/2/2011	124	653	5.3	4	16	2.09 ± 1.4	8.8 ± 11.5
77129	EG	BAR	6/7/2008	5/15/2009	342	3491	10.2	5	61	2.13 ± 1.73	9.6 ± 17.5
77130	EG	BAR	11/9/2008	9/19/2009	314	2489	7.9	5	76	2.2 ± 1.76	8.6 ± 12.6
77130a	EG	BAR	10/4/2009	6/4/2010	243	2140	8.8	5	78	1.86 ± 1.5	6.5 ± 10.8
77132	EG	BAR	6/7/2008	5/30/2009	357	2601	7.3	3	35	2.01 ± 1.94	15.5 ± 25.4
77132a	EG	BAR	8/13/2009	4/14/2010	244	2090	8.6	2	12	2.15 ± 0.46	14.8 ± 27.3
7713301	EG	STR	12/4/2008	4/27/2009	144	1506	10.5	5	40	1.83 ± 1.2	4 ± 5.1
7713302	EG	JOZ	5/4/2012	2/19/2013	291	3009	10.3	3	27	2.81 ± 2.17	15.7 ± 23
77134	EG	STR	12/1/2008	7/29/2010	605	5330	8.8	4	19	3.28 ± 2.47	24.2 ± 28.8
77134a	EG	STR	8/19/2010	5/2/2011	256	2561	10.0	5	17	2.04 ± 2.16	19.2 ± 29.9
77134b	EG	STR	7/22/2011	4/12/2012	265	2401	9.1	3	8	2.08 ± 1.66	47.1 ± 46.2
77135	EG	STR	12/1/2008	2/8/2011	799	8522	10.7	4	107	2.5 ± 2.82	11.5 ± 18

In my analysis of environmental predictors of $mFPT_{Rmax}$, the most parsimonious model with the highest support included difference in NDVI over a 32 day lag, difference in rainfall over a 32 day lag, and geographical location for both Egyptian Geese and Red-billed Teal (Table 4.4). Following the AIC criteria and model selection procedure I employed, model 34 had the greatest support and suggested that variation in $mFPT_{Rmax}$ was best explained by changes food quality, amount of rainfall, and the geographical location of individuals. The variances explained by the fixed effects (marginal R^2) of the chosen models were 9.4 and 11.3%, while the variances explained by both fixed and random effects (conditional R^2) were 17.2 and 13.1% for Egyptian Geese and Red-billed Teal respectively (Table 4.5). The individual level variability was noticeably higher in Egyptian Geese (7.8%) compared to that of Red-billed Teal (1.8%). The candidate models representing the reactive movement

hypothesis were noticeably absent from the top four and nine movement models of Egyptian Geese and Red-billed Teal respectively.

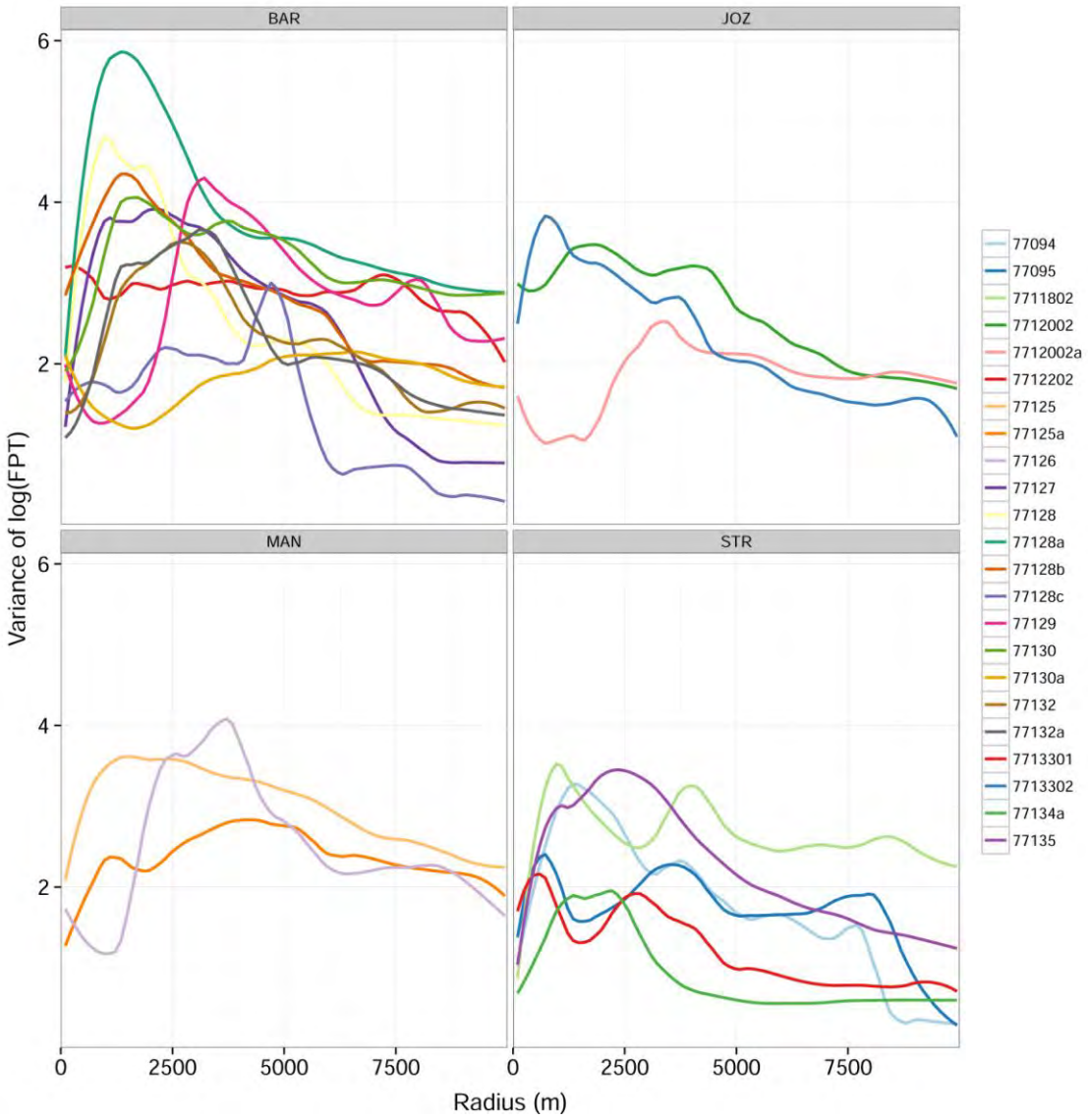


Figure 4.4 Curves of individual Egyptian Geese showing the variance in log first-passage time against circle radius. Panels correspond to individuals tagged at 4 different wetland sites. PTT, transmitter identity; BAR, Barberspan; STR, Strandfontein; MAN, Lake Manyame; JOZ, Jozini Dam.

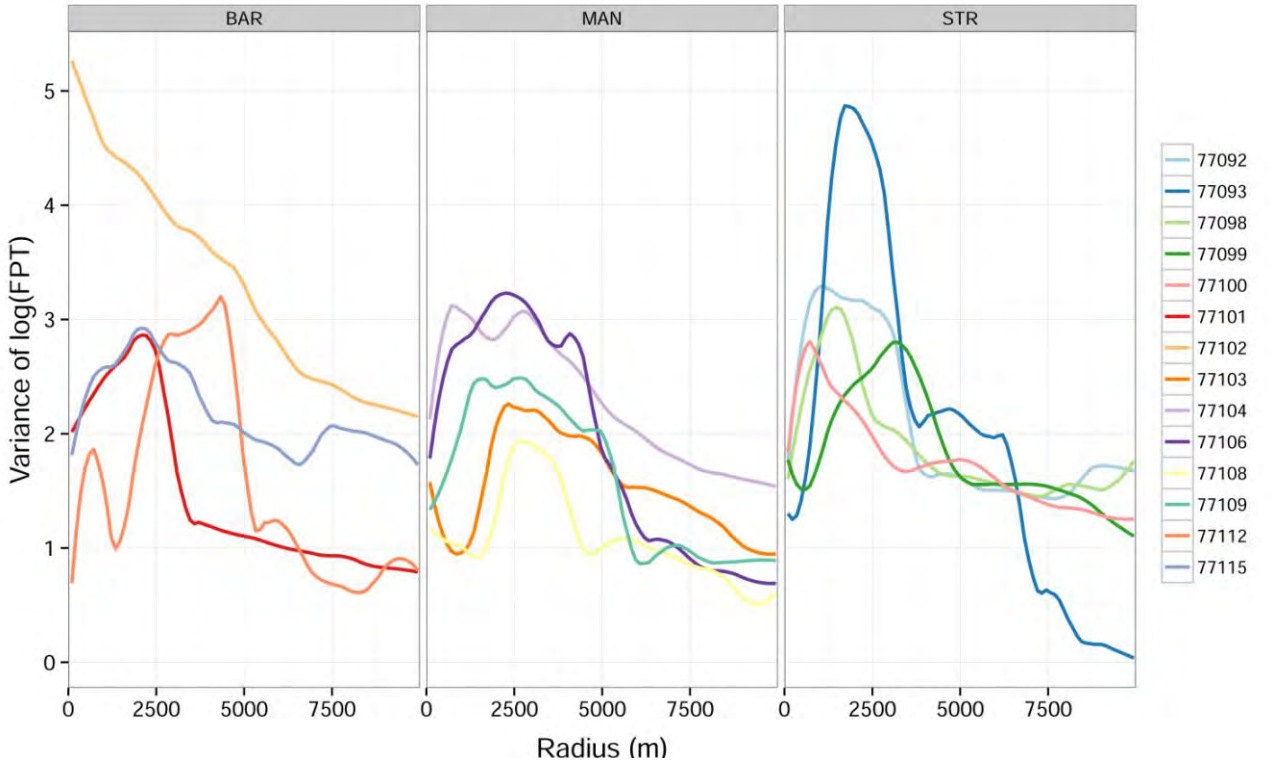


Figure 4.5 Curves of individual Red-Billed Teal showing the variance in log first-passage time against circle radius. Panels correspond to individuals tagged at 3 different wetland sites. PTT, transmitter identity; BAR, Barberspan; STR, Strandfontein; MAN, Lake Manyame.

For Egyptian Geese, differences in both NDVI and rainfall in the 32 days prior to arrival were significantly and positively correlated with $mFPT_{Rmax}$, supporting predictions PM_1 and PM_2 (Fig. 4.6 & Table 4.5). The magnitude of the effect of rainfall was three times higher than that of NDVI. Individuals from the Strandfontein population had a significantly higher $mFPT_{Rmax}$ than those of the Barberspan, which was the reference category. The parameter estimates for birds from Jozini and Lake Manyame were not significantly different from zero. For Red-billed Teal, the difference in NDVI during the 32 days prior to arrival was negatively correlated to $mFPT_{Rmax}$ while rainfall was significantly and positively correlated with FPT (Table 4.5). Again the magnitude of the effect of rainfall was higher than that of NDVI. Individual teal from the Strandfontein population had a significantly higher $mFPT_{Rmax}$ than those of the Barberspan population, while parameter estimates for birds from Lake Manyame were not significantly different from zero. I found little support for effects of temperature, elevation or mNDWI in explaining variation in FPTs There was little evidence of spatial autocorrelation in the semi-variograms and bubble plots. The kappa statistic was less than 10 for models of both species, indicating an absence of collinearity in the predictor variables.

Table 4.4 Comparisons of the top models (ΔAICc < 20) of first-passage time as a function environmental variables of two waterfowl species in southern Africa. Models are ranked based on differences in the corrected Akaike's Information Criteria (ΔAICc) Akaike weights (AIC_c Wt). K is the number of estimated parameters and Cum Wt is the cumulative weight of sequential models.

Model		K	AICc	ΔAICc	AICc Wt	Cum Wt
	Egyptian Geese					
32	FPT ~ $\Delta NDVI_{t-32}$ + $\Delta mNDWI_{t-32}$ + $\Delta Precip_{t-32}$ + site + (1|BirdID)	9	1979.25	0.00	0.43	0.43
34	**FPT ~ $\Delta NDVI_{t-32}$ + $\Delta Precip_{t-32}$ + site + (1|BirdID)**	**8**	**1979.39**	**0.14**	**0.40**	**0.83**
30	FPT ~ $\Delta NDVI_{t-32}$ + $\Delta Precip_{t-32}$ + (1|BirdID)	5	1982.95	3.70	0.07	0.90
28	FPT ~ $\Delta NDVI_{t-32}$ + $\Delta mNDWI_{t-32}$ + $\Delta Precip_{t-32}$ + (1|BirdID)	6	1983.44	4.19	0.05	0.95
19	FPT ~ $mNDWI_t$ + $Precip_t$ + site + (1|BirdID)	10	1984.52	5.27	0.03	0.98
16	FPT ~ $NDVI_t$ + $mNDWI_t$ + $Precip_t$ + site + (1|BirdID)	11	1986.00	6.75	0.01	1.00
15	FPT ~ $mNDWI_t$ + $Precip_t$ + (1|BirdID)	5	1992.27	13.02	0.00	1.00
	Red-billed Teal					
34	**FPT ~ $\Delta NDVI_{t-32}$ + $\Delta Precip_{t-32}$ + site + (1|BirdID)**	**7**	**833.87**	**0.00**	**0.38**	**0.38**
26	FPT ~ $\Delta NDVI_{t-16}$ + $\Delta Precip_{t-16}$ + site + (1|BirdID)	7	834.79	0.92	0.24	0.62
32	FPT ~ $\Delta NDVI_{t-32}$ + $\Delta mNDWI_{t-32}$ + $\Delta Precip_{t-32}$ + site + (1|BirdID)	8	835.21	1.34	0.19	0.82
24	FPT ~ $\Delta NDVI_{t-16}$ + $\Delta mNDWI_{t-16}$ + $\Delta Precip_{t-16}$ + site + (1|BirdID)	8	836.83	2.95	0.09	0.90
30	FPT ~ $\Delta NDVI_{t-32}$ + $\Delta Precip_{t-32}$ + (1|BirdID)	5	837.70	3.83	0.06	0.96
28	FPT ~ $\Delta NDVI_{t-32}$ + $\Delta mNDWI_{t-32}$ + $\Delta Precip_{t-32}$ + (1|BirdID)	6	839.54	5.67	0.02	0.98
22	FPT ~ $\Delta NDVI_{t-16}$ + $\Delta Precip_{t-16}$ + (1|BirdID)	5	840.40	6.53	0.01	0.99
20	FPT ~ $\Delta NDVI_{t-16}$ + $\Delta mNDWI_{t-16}$ + $\Delta Precip_{t-16}$ + (1|BirdID)	6	842.45	8.57	0.01	1.00
35	FPT ~ $\Delta mNDWI_{t-32}$ + $\Delta Precip_{t-32}$ + site + (1|BirdID)	7	852.07	18.19	0.00	1.00

Table 4.5 Summary of the generalised mixed models with the highest support in the analysis of first-passage time (FPT) as a function of environmental variables. R^2 values are measures of model fit based on fixed effects only (marginal variance, $R^2_{GLMM(m)}$) and on the full model including random effects (conditional variance, $R^2_{GLMM(c)}$).

	Parameter	β	Lower CI	Upper CI	SE	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$
Egyptian Geese						9.4%	17.2%
	(Intercept)	1.34	1.24	1.45	0.06		
	ΔNDVI t-32	0.04	0.01	0.06	0.02		
	ΔPrecipt-32	0.12	0.09	0.14	0.02		
	Site : JOZ	0.04	-0.14	0.23	0.11		
	Site : MAN	-0.13	-0.33	0.07	0.12		
	Site : STR	0.25	0.10	0.40	0.09		
No. of observations: 1165, random effect groups: ID, 29							
Red-billed Teal						11.3%	13.1%
	(Intercept)	1.59	1.47	1.71	0.07		
	ΔNDVI t-32	-0.06	-0.11	-0.01	0.03		
	ΔPrecipt-32	0.16	0.12	0.21	0.03		
	Site: MAN	-0.12	-0.27	0.03	-0.11		
	Site: STR	0.24	0.08	0.39	0.09		
No. of observations: 445, random effect groups: ID, 14							
	*Reference site: BAR						

4.5 Discussion

My findings show little evidence for the reactive movement hypothesis; instead, waterfowl appeared to respond to shifts in resource conditions in a given area based on changes in magnitude and direction of environmental variables between preceding lag periods and current periods of occupation. This suggests that movement decisions were potentially more complex than those that would result from randomly sampling the landscape and ceasing movement when suitable conditions were encountered. While it may be difficult to identify

exactly how waterfowl perceive their landscapes, spatial awareness and prior experience may be mechanisms that might allow waterfowl to capitalise on high quality resources. Egyptian Geese spent more time in areas which had increased primary productivity and associated increases in rainfall in the 32 day period leading up to goose arrival; results which were consistent with predictions PM_1 and PM_2. The magnitude of the effect of rainfall was stronger than that of NDVI. By contrast, Red-billed Teal spent more time in areas in which primary productivity had decreased over the previous 32 days and where rainfall had increased, consistent with PM_2 but not with PM_1. Again, rainfall had a stronger effect than NDVI. Geographical location (site variable) of individuals was a significant predictor of waterfowl movement behaviour; individuals of both species had higher mean FPTs in the Strandfontein populations compared with the Barberspan populations. Temperature and elevation had no significant effect on FPT. These findings suggest both that thermoregulatory constraints do not play a role in structuring movements and that movements are not clustered in coastal regions of southern Africa. The environmental variable that represented a change in wetland extent (ΔmNDWI) appeared in several of the competing models, but was not included in the final model with the highest support. This indicates that there is a potential effect of either filling or drying of wetlands on FPT, however these dynamics do not dominate the way in which waterfowl movements are structured.

The moderate amount of variance explained by the models could have resulted from several unmeasured factors affecting landscape use. For instance, waterfowl form large aggregations outside of breeding periods, and so social factors such as competition may affect the choice of habitat used. Human disturbance and predation pressure are also likely to significantly influence habitat choice and movements (Cumming et al. 2016). Another potential issue which might have influenced the explained variance is the choice of method used to delineate the geographic area over which environmental conditions were measured. I used the widely adopted movement-based KDE method which has its foundation in point-based methods. Traditional KDE methods, however, may significantly underestimate the size of utilisation distributions (Fleming et al. 2014, 2015). Measuring environmental variables over a broader spatial extent would, therefore, change the calculated landscape conditions that the waterfowl would have experienced. In turn, this has the potential to alter the outcomes of the first-passage time models.

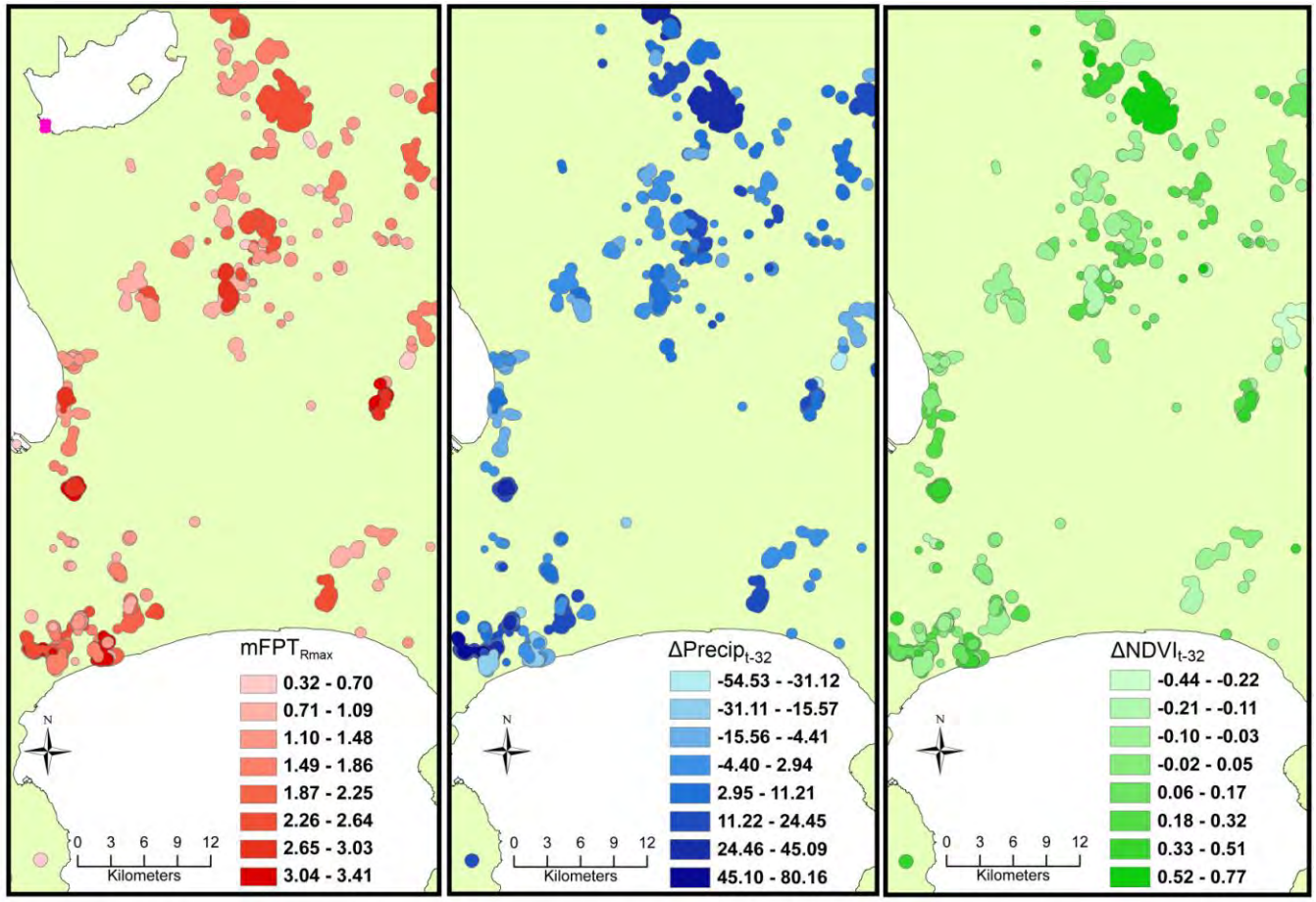


Figure 4.6 Three panels which represent a gradient of mean values of mean first-passage time ($mFPT_{Rmax}$) and environmental variables within utilisation distribution polygons. These data illustrate the positive relationship between FPT and a 32-day lag in NDVI and precipitation (e.g. dark red, dark green and dark blue polygons represent sites at which FPT and environmental variables were strongly positively correlated). $\Delta NDVI_{t-32}$, the difference between mean NDVI within a polygon at time *t* and *t-32days*; $\Delta Precip_{t-32}$, the difference between precipitation within a polygon at time *t* and *t-32days* measured in mm. Note that $mFPT_{Rmax}$ was measured in hours and has been logged transformed.

My findings that higher FPTs of Egyptian Geese are a response to increases in primary productivity, as opposed to standing biomass, are in accordance with several studies of migratory movements of herbivorous waterfowl occurring at high latitudes in the northern hemisphere. These movements are linked to plant phenology and follow the predictions set out by the GWH, which states that waterfowl time their spring migration to take advantage of successive peaks of forage quality along their migration routes (Bos et al. 2005, van der Graaf et al. 2006, 2007, van Wijk et al. 2012, Shariatinajafabadi et al. 2014). Although semi-nomadic waterfowl, living in low productivity environments where the distribution of resources is patchier (Roshier et al. 2001), have different constraints in terms of locating resources to those of migrants (i.e. lack of distinct and predictable seasonal changes), they seem to prioritise forage quality in a similar manner. Responding to such changes, however, requires that waterfowl have some sort of prior knowledge of the state of landscape resources and do not simply perform random searches through the landscape to settle where conditions are suitable.

For birds living in semi-arid areas, there are trade-offs between when to stay and when to leave an area (Dean et al. 2009). The ability of waterfowl in my study system to possess spatial awareness could allow them to capitalise on highly nutritious food sources and leave areas when nutritional quality starts to decline, providing an adaptive advantage through periods of resource uncertainty. The role of spatial memory in movement has recently received attention (Mueller and Fagan 2008b, Van Moorter et al. 2009, Fagan et al. 2013, Seidel and Boyce 2015) and there are indeed fitness benefits of memory in heterogeneous landscapes of intermediate complexity. Waterfowl may employ a similar strategy to that of other nomadic birds (e.g., Snail Kites (Bennetts and Kitchens 2000) and Pacific Black Ducks (Mcevoy et al. 2015)) in that exploratory movements are adopted through periods of high resource abundance. This would allow waterfowl to attain a level of familiarity with high quality resource patches, avoiding the need to search extensively when resource abundance is low. Memory and prior knowledge therefore have the potential to be particularly relevant to waterfowl movement strategies in arid landscapes (Roshier et al. 2008a). Indeed, in this study Egyptian Geese adopted behaviour that allowed them to respond to food quality in a similar manner to that of migrant geese following the green wave.

Kingsford et al. (2010) developed a conceptual model of the movement, breeding and feeding response of five arid-zone waterbird functional groups (dabbling and diving ducks, herbivores, piscivores, large waders and small waders). They proposed that grazing and

dabbling (or invertebrate) feeders should have different temporal responses to rainfall and wetland filling events. Dabbling ducks should arrive first to take advantage of invertebrates which have hatched following wetland inundation, while grazers should lag in their response to capitalise on terrestrial or aquatic plants which grow and germinate more slowly. Egyptian Geese responded to rainfall at a 32 day lag period which is what I would expect for a grazing bird feeding on emergent vegetation on freshly exposed shorelines.

Observational studies of Red-billed Teal responses to rainfall events in southern Africa support ideas that invertebrate feeders should respond quickly (Simmons et al. 1999, Herrmann et al. 2004). Data from longer term studies, however, suggest that this peak in abundance occurs at a much longer lag period, with a peak occurring at 4 months post rainfall (Cumming et al. 2012b). My finding that teal responded to rainfall at a 32 day lag rather than a 16 day lag might be explained by their niche breadth. Petrie (1996) showed that teal have considerable dietary flexibility. During energetically demanding periods such as the breeding season, for example, invertebrate consumption was < 14% of total food items while the majority of remaining energy requirements was satisfied by the consumption of native grass seeds which surround wetlands. The relationship between NDVI and FPT in Red-billed Teal was opposite to that found in Egyptian Geese. First-passage time was higher in areas in which primary productivity had decreased over a 32 day lag period. It is possible that there was a higher abundance of grass seeds available as growth decreased, providing teal with an adequate food resource. These results suggest that responses to rainfall events vary considerably across apparently similar arid zone landscapes and that dietary flexibility may drive changes in movement responses between species.

One question that remains enigmatic is which cues waterfowl use to detect distant rainfall events. It has been proposed that they might be able to sense rain fronts, but the evidence that waterfowl respond to lag variables and not immediate conditions suggests that they have some knowledge of landscape conditions and can make decisions based on environmental cues (Mcevoy et al. 2015). There is evidence of a similar response in other species. Red-billed Quelea *Quelea quelea*, small granivorous passerines in southern Africa, are able to respond to dynamic changes in resources (Cheke and Tratalos 2007); they appear to move ahead of rainfall events and then track back towards areas in which rain has fallen to take advantage of grass seeds.

Both Egyptian Geese and Red-billed Teal had higher than average FPTs in utilisation distributions in the Strandfontein population than in the Barberspan population. Although

there was no significant difference between the other sites, Jozini had slightly higher FPT than Barberspan while the Lake Manyame population had slightly lower average FPT (Table 4.5). It is interesting to note that the direction and magnitude of these patterns were consistent between both these species, which indicates the important influence of landscape conditions on movement in comparison to differences in life history and ecological traits between the two species. Differing responses to environmental variation by populations of a species has been shown in several instances (Singh et al. 2010, 2012, Mandel et al. 2011). This follows a theoretical prediction that increased variation of movement responses within a species range should be associated with increased variability of resources at broad landscape scales (Roshier et al. 2008b, Singh et al. 2012, Mcevoy et al. 2015). This is indeed evident in my study as Barberspan and Strandfontein occur in noticeably different landscapes. Barberspan lies in an arid summer rainfall region, whereas Strandfontein is a winter rainfall region with less variability in the timing and amount of precipitation (Fig. 4.7). The landscape surrounding Strandfontein is characterised by a high density of grain producing agricultural land. Associated with these farms are small dams used for storage, many of which have stable water levels throughout the year. On the other hand, areas into which many of the individuals from the Barberspan population moved were more arid, with agricultural land separated by semi-deserts (Figs. 4.1, 4.2 & 4.7). Spatiotemporal correlation of resources was thus higher near Strandfontein and could mean there is less need for waterfowl to move long distances, resulting in higher first-passage times. This illustrates the range in strategies of nomadic movement, which is proposed to be an outcome of spatiotemporal correlation in landscape resources (Jonzén et al. 2011). Differences in movement behaviour (measured by, for example, parameters such as daily movement rates, distance moved, turning angles) in these populations has previously been demonstrated by Cumming et al. (2012a), indicating that populations of Egyptian Geese at Barberspan and Strandfontein move in different ways, while little separated the movements of different populations of Red-billed Teal. In my analyses, however, the data showed clear differences in patterns of FPT (Figs. 4.4 & 4.5, Table 4.1). This suggests that analysing movements in the FTP framework can provide new as well as complementary insights into existing drivers of waterfowl movement. Additionally, it is important to recognise the variation of individuals within the same population in understanding population level processes (Doerr and Doerr 2005b, Hawkes 2009).

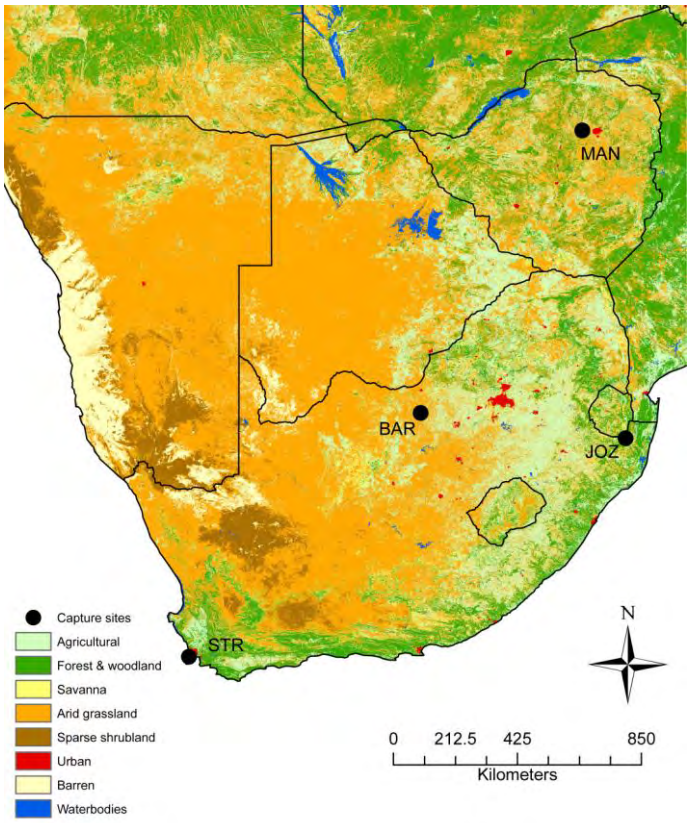


Figure 4.7 Land cover classes within the southern African landscape. Points represent capture sites for sampled individuals. BAR, Barberspan; JOZ, Jozini Dam; MAN, Lake Manyame; STR, Strandfontein.

I was able to undertake the first quantitative analysis of the interaction between external factors and navigational capacity of southern African waterfowl in the context of a current movement ecology framework. More generally, I have shown the utility of linking long term telemetry data over broad geographic scales with environmental conditions experienced by multiple individuals to uncover the proximate drivers of waterfowl movement. The analysis of movement using the FPT method allowed us to conclude that waterfowl movements in southern Africa are a response to the dynamics of rainfall and primary productivity. In addition, my findings suggest that waterfowl movements are not simply reactive but rather involve mechanisms which allow waterbirds to integrate information of the local landscape in order to take advantage of productive habitats. Future research should take the form of a more detailed analysis of movement and changes in resources to further understand the mechanism underlying the prescient movement hypothesis.

5 CAN BIRD SPECIES WITH DIFFERENT MOVEMENT PATTERNS AND FUNCTIONAL TRAITS OCCUPY SIMILAR ECOLOGICAL NICHES?

5.1 Abstract

Movement is one way in which birds respond to variability in landscape resources, allowing them to meet the ecological needs necessary for reproduction and survival. It is, however, unclear how movement influences the niche dimensions of highly mobile species, particularly when they co-exist in spatially and temporally heterogeneous communities. I used RLQ (R-mode linked to Q-mode) and fourth-corner analyses within a functional trait framework to investigate the inter-relationships between three waterbird trait groupings (movement, dietary and foraging habitat) and four environmental variable groupings (rainfall, land cover, vegetation structure and water quality) from 60 wetland sites, sampled seven times each at bimonthly intervals, in KwaZulu-Natal, South Africa. Specifically, I tested whether the scale of landscape variables filtered movement traits and whether these traits operated in conjunction with dietary and foraging habitat traits to form distinct ecological niches in waterbirds. Results of the fourth-corner analysis showed that movement ability does indeed relate to scale of resources, in that more mobile species (migrants and nomadic birds) responded to broad scale landscape characteristics (rainfall and land cover). There was evidence of clear ecological niche separation between residents and migrants. A migratory trait syndrome grouped with an invertebrate diet and short vegetation foraging habitat and was associated with wetlands surrounded by a high proportion of natural vegetation and short shoreline vegetation. Resident and local movers tended to be carnivorous and associated with large wetlands with high salinity and pH. I concluded that the scale of landscape resources can act as a filter of movement traits, and that in conjunction with dietary and foraging traits, waterbirds with different movement patterns occupy distinct ecological niches.

5.2 Introduction

One of the most fundamental challenges faced by living organisms is that of obtaining sufficient resources to remain alive, reproduce and recruit. Most heterotrophs have responded to this challenge by either living in an environment through which food moves (e.g., a river or a rocky shore) or by developing ways of moving to their food. Movement helps organisms to respond to resource variation in space and time and offers an alternative to dormancy as a strategy for persisting though periods of hardship (Chesson and Rosenzweig 1991). In particular, flying organisms, such as birds and bats, have evolved the capacity to move long distances with proportionally little energy expenditure.

Possessing superior movement ability should in theory allow a given species to exploit richer patches where resources are not limiting, and hence to reduce competitive interactions with other individuals of the same species. At the same time, however, highly mobile individuals may arrive simultaneously at the same solution to a given environmental problem and reach much higher local densities – and encounter much stronger competition - than would be possible for a less mobile organism. By virtue of integrating across a wider area, mobile species are also more likely to encounter localised species that have similar resource needs. Mobile species should therefore find a foraging strategy that exploits environmental variation without bringing them too directly into competition with conspecifics and other similar species, both mobile and less mobile. The ways in which meeting these demands will modify the niche of both mobile species and the more local species that they encounter are, however, poorly understood.

In birds, movements can occur across a wide range of spatiotemporal scales and birds have adopted a continuum of movement strategies that range from residence to migration (Alerstam et al. 2003). Distances travelled by birds annually vary from a few kilometres to over 10 000 km for a Palearctic migrant. Between these two extremes, various other modes of movement exist, including local movement, nomadic movement, and altitudinal movement (Roshier and Reid 2003). Furthermore, individuals between and within populations, and those at different life stages, can adopt a combination of movement modes, thus creating difficulties in assigning a particular species to a single movement mode (Jahn et al. 2004, Dingle and Drake 2007).

Much research has been devoted to understanding the mechanisms that allow avian migrants and residents to co-exist on the non-breeding grounds (Greenberg 1995, Johnson and Sherry 2005). There is evidence that long distance migratory birds keep a tight niche association throughout the year, so called "niche-tracking" (Joseph and Stockwell 2000), while other species exhibit "niche-switching" (Nakazawa et al. 2004). Several mechanisms could explain these patterns; for instance, competition with residents on the non-breeding grounds might force migrants to use alternative food resources, habitats or niches (Pérez-Tris and Tellería 2002, Boyle et al. 2011). This could have important implications for survival and subsequent breeding output in that the quality of, and access to, resources on the wintering grounds may adversely reproduction on the breeding grounds (Pérez-Tris and Tellería 2002, Studds and Marra 2005). However, generalities surrounding competitive interactions are, in many cases, not consistent. For instance, studies of insectivorous passerines provide evidence that residents (rather than migrants) display a shift in foraging niche to reduce the effects of seasonal resource competition (Jedlicka et al. 2006).

The study of functional traits provides one method for identifying and characterising ecological niches of organisms with different movement capabilities. It has long been recognised that species have evolved within the limitations of environments, and so functional and life history traits are filtered by a specific set of habitat and environmental conditions (Wiescher et al. 2012). Instead of examining the response of a single species, focusing on the distribution of functional traits within an animal community across environmental gradients allows for a deeper understanding of the mechanisms structuring animal communities (McGill et al. 2006).

I used an unusually intensive data set on waterbird communities, together with two recently developed statistical approaches, to explore the inter-relationships between waterbird functional traits and environmental characteristics in wetlands on the coastal plain of KwaZulu-Natal, South Africa. I hypothesized that variation in resource availability might allow migratory and nomadic birds to exploit the same resources as resident birds while effectively using the broader landscape at a different spatial scale. Alternatively, despite moving at different scales, local competition for resources (and/or other causes) might lead to niche divergence between species with different movement capabilities. I did not measure competition directly, but rather differentiated between the two hypotheses using three groups of functional traits (movement, diet, and foraging habitat) that were related to four groups of environmental variables (vegetation structure, water quality, rainfall and land cover type).

Most previous studies of species-environment-function relationships have used a two-step approach; species are first assigned to a particular group/guild, and then these groups are related to environmental factors (Dolédec et al. 1996). It is difficult to know which trait characteristics groupings to use, and changes in habitats may elicit responses that are detectable in one group but not in others. RLQ analysis (Dray and Legendre 2008), a relatively new analytical technique, overcomes these challenges by considering all traits simultaneously, without the need to assign species to a group based on a single life history trait. This analysis relies on the following three data tables (*rows x columns*): (1) L (*n* x *p)* which describes the abundance of *p* species at *n* sampling sites; (2) R (*n* x *m*) describing *m* environmental measurements for *n* sample sampling sites; and (3) Q (*p* x *s*) describing *s* functional traits for *p* species.

Recent implementations of this method have been used to describe relationships between traits and habitat characteristics. However, the latest version of these methods (Dray et al. 2014) now allows for these relationships to be quantified using statistically rigorous permutation tests. Examples of studies using these methods examine responses of avian traits to the effects of urbanisation, landscape fragmentation and changes in woody vegetation cover (Seymour and Dean 2010, Ikin et al. 2012, 2014); as far as I am aware, this is the first study to apply them to the question of the scale of movement and resource selection.

My first objective was to explore the relationship between scales of movement and environmental variables. Species differ in their abilities to sense and respond to spatial heterogeneity in resources across a range of scales; movement capability can play an important role in structuring this response. Compared to migrants, residents and local movers may not be able to respond to spatial variability at larger scales. It has been suggested that movement ability is therefore closely linked to the scales at which landscape resources are structured and distributed (Jonzén et al. 2011). Focusing on landscape patterns of resource distribution, rather than a limited set of food resources or habitat characteristics, can provide a productive avenue for understanding the spatiotemporal scales which are relevant for structuring of waterbird communities (Pavey and Nano 2009). There is a hierarchy in movement traits from broad (migrants) to fine (residents) scale. In a similar manner, habitat variables range from broad (rainfall and land cover) to fine (vegetation structure and water quality). For this objective I hypothesised that if the spatial scale of environmental variables was an important filter of movement capability, then broad scale environmental variables would be associated with migrants and nomads, while fine scale variables would be

associated with residents and local movers. The second objective of the analysis was to determine whether movement traits, in combination with diet and foraging traits, were associated with environmental variables. Evidence of distinct groups would indicate separation in ecological niches of birds employing different movement modes, thus testing my primary hypothesis.

5.3 Methods

5.3.1 Overview

I quantified variation in both space and time in waterbird community composition over a 14-month period, undertaking point counts of birds at each of 60 different wetland sites every two months (i.e., 7 times per wetland, to give a total of 420 different counts). I also measured a range of environmental variables at each wetland after each count. I analysed the resulting data using three analytical methods in a step-by-step sequence (Fig. 5.1) to both test my hypothesis and further explore the relationship between functional traits (movement, dietary, and foraging habitat) and environmental variables (vegetation structure, water quality, land cover and rainfall). First, RLQ analysis was used to assess significance of the global relationship between species abundances, environmental variables and waterbird functional traits (step 1, Fig. 5.1). Second, bivariate fourth-corner tests were performed to test the hypothesis that the scale of environmental variables filters movement functional traits. Fourth-corner results were also used to see whether dietary and foraging traits are associated to environmental variables in conjunction with movement traits (step 2, Fig. 5.1). Third, fourth-corner tests were directly applied to the multivariate RLQ ordination to test whether functional traits were significantly correlated with RLQ axes and whether traits clustered with specific habitat conditions to create distinct ecological niches in waterbirds (step 3, Fig. 5.1).

5.3.2 Study area

The study was undertaken on the coastal plain of KwaZulu-Natal, South Africa. The study sites included 60 wetland sites across 14 wetlands (Figure 2.3). Sites were grouped according to wetland clusters. See Chapter 2 for full details of study area and wetland clusters.

5.3.3 Sampling protocol

Standardised bimonthly waterbird point counts at 60 sites across the study area were carried out from April 2012 to June 2013. This resulted in 7 sampling replicates for each of the 60 sites. See Chapter 2 for details of counting protocol. Four groups of environmental variables were measured at each site during each sampling period (Table 5.1). These were vegetation structure (shoreline and aquatic), water quality, rainfall (at 3 monthly lag periods) and proportion of three land cover classes in a 3 km buffer surrounding each sampling site. See Chapter 2 for derivation of and sampling protocol for each variable. Summary of environmental variable values for each wetland cluster are shown in Tables 2.3 to 2.6.

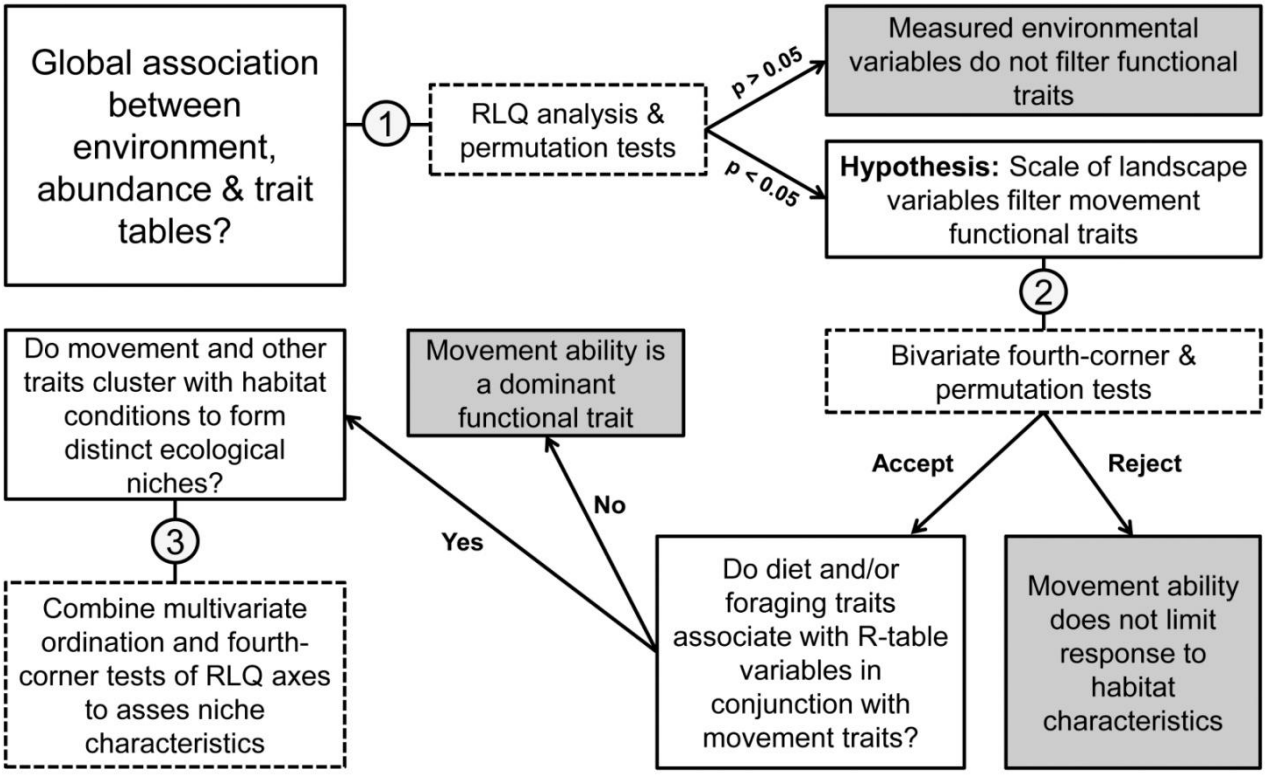


Figure 5.1 Flowchart illustrating hypotheses, questions and sequential analytical steps (1-3) carried out to explore the relationship between functional traits and environmental variables in waterbirds. Each sequential step consists of a hypothesis or question (solid lined box), a statistical test (dotted lined boxes), and potential alternative explanations (grey filled boxes). Arrows represent the possible outcomes of analytical tests.

5.3.4 Species and functional traits

Birds that were not strictly ecologically dependent on wetlands (e.g., passerines such as sparrows that are also common in terrestrial habitats) and birds recorded in less than 10% of counts were excluded from the analysis. Subsequently, the analysis included 53 species from 15 families (section 5.6 Appendix 1).

For each species, I measured 12 functional traits associated with diet, movement, and foraging habitat (Table 5.2). Species were assigned to one of four foraging guilds (deep water, emergent vegetation, shallow water, short vegetation) based on an existing ecological knowledge and an established functional classification (Cumming et al. 2012b). Classifications of movement (inter-African migrant, intra-African migrant, nomad, resident, local mover) and dietary (invertebrates, carnivorous, herbivorous) traits were based on species descriptions in Roberts Birds of Southern Africa (Hockey et al. 2005). Note that inter-African migrants are species that move between Europe/Asia and Africa. Species could belong to multiple functional groups (e.g. a single species could display both resident and local movement behaviour, and feed on a combination of plant and animal matter), and so traits were coded in binary format. See Appendix 1 for details of species classification.

Table 5.1 Abbreviations, units and derivations of environmental variables measured at each sampling site.

Variable group	Variable code	Details
Vegetation	AQ-RS	Proportion of aquatic reed and sedge vegetation
	AQ-FG	Proportion of flooded grass vegetation
	AQ-SF	Proportion of emergent, submerged and floating vegetation
	SL-RS	Proportion of shoreline reed and sedge vegetation
	SL-GM	Proportion of shoreline grass and mudflats
	SL-TS	Proportion of shoreline trees and shrubs
Water quality	pH	Standard units
	DO	Dissolved oxygen ($mg.L^{-1}$)
	Sal	Salinity (psu)
	Temp	Water Temperature (°C)
Rainfall	Rain 1	Monthly rainfall at a one month lag prior to bird counts
	Rain 2	Monthly rainfall at a two month lag prior to bird counts
	Rain 3	Monthly rainfall at a three month lag prior to bird counts
Land cover	ANTHRO	Rural, agriculture, urban
in 3km buffer	NAT	All natural vegetation classes (Bushveld, grassland, etc)
around count site	WET	Wetlands (both fresh and estuarine)

Table 5.2 Descriptions and abbreviations of functional traits measured for each species.

Variable group	Variable code	Details
Foraging	DEEP	Species that forage over or in deep water (> ca. 2m)
	EMERGE	Species that forage in emergent vegetation including reeds and other macrophytes
	SHALLOW	Species that forage in shallow water (< ca. 2m)
	SHORT	Species that forage in short vegetation, grass or mudflats
Movement	Inter.M	Inter-African migrant
	Intra.M	Intra-African migrant
	Nomad	Nomad
	Resident	Resident
	Local	Local movement
Diet	INVERT	Invertebrates
	CARN	Carnivorous
	HERB	Herbivore

5.3.5 Statistical analyses

RLQ and fourth-corner analyses, which are both three-table methods, have been described as state-of-the-art multivariate methods for detecting relationships between functional traits and environmental variables (Dolédec et al. 1996, Legendre et al. 1997, Dray and Legendre 2008). These analyses rely on the following three tables (*rows x columns*): (1) L (*n* x *p)* which describes the abundance of *p* species at *n* sampling sites; (2) R (*n* x *m*) describing *m* environmental measurements for *n* sample sampling sites; and (3) Q (*p* x *s*) describing *s* functional traits for *p* species.

As a first step, ordinations (either correspondence analysis, principal components analysis or Hill-Smith analysis depending on the qualitative or quantitative nature of the data) on each table are carried out separately with the aim of understanding how species communities are organised, which environmental gradients are present, and which trait syndromes exist (Dray and Legendre 2008). The next step in the RLQ analysis combines the three ordinations via co-inertia techniques (Dray et al. 2003) to identify the primary relationships between environmental characteristics and functional traits which are mediated

by species abundances at sampling sites. A multivariate statistic, which is equal to the sum of RLQ eigenvalues, can be used to test the significance of the global association between the three tables (Dray et al. 2014)

Fourth-corner analysis uses the same three tables with the aim of detecting univariate correlations between each combination of trait-environment variables, using two sequential permutation models. The first model tests the null hypothesis that there is no link between the environmental variables and species abundances (R and L tables). If the null hypothesis is rejected then the second model is applied to test the null hypothesis that assumes there is no link between species abundance and functional trait characteristics (L and Q tables). The association between a trait and environmental variable is then considered significant when the largest of the p values from both models is lower than a specified alpha threshold. Due to the high number of correlation tests, the procedure calculates adjusted p values based on the false discovery rate (FDR) method (Benjamini and Hochberg 1995).

Traditionally RLQ and fourth corner analysis have been implemented separately and there are drawbacks to each approach (Dray et al. 2014). RLQ analysis does not allow for tests of statistical significance between each trait-environment variable, while fourth-corner analysis does not consider the covariation between traits and environments themselves. Dray et al. (2014) proposed a framework for jointly implementing these complementary methods, which applies fourth-corner tests directly onto the RLQ axes. RLQ scores are used as variables in the fourth-corner analysis instead of the raw data, which allows one to test the associations between environmental gradients-trait scores and environmental scores-traits syndromes in multivariate ordination space.

Water quality readings from August 2012 were unavailable and to standardise the format of data tables, all bird, vegetation and rainfall data from these periods were excluded from the RLQ analysis. As a result, the data used in this analysis consisted of an R matrix (356 point counts x 16 environmental variables), L matrix (356 point counts x 53 species) and Q matrix (12 functional traits x 53 species). See Tables 5.1 & 5.2 for summary and codes of environmental variables and functional traits. Species abundances were log-transformed and environmental variables were standardised prior to inclusion in the analysis. All permutation tests were carried out using 49,999 iterations. Analyses were carried out in R statistical software version 3.0.2 using the *ade4* package (Dray and Dufour 2007).

5.4 Results

5.4.1 Global association between environment, abundance and trait tables

Results of the RLQ permutation tests showed that there was a strong significant relationship between the species abundances, environmental variables and functional trait tables ($p < 0.01$; step 1, Fig. 5.1). The first two axes of the RLQ ordination accounted for 80.4% of the variance in the co-structure of the three tables (Table 5.3). The variance in the separate correspondence analysis of environmental variables was well preserved in the first and second RLQ axes (93.1% and 81.4% respectively). The variance in the separate principal components analysis of the species abundance table was well preserved in the first RLQ axis (56.3%) but less so in the second axes (31.8%). The variance in the separate Hill-Smith analysis of functional traits was well preserved in both RLQ axes (57.5% and 79.2% respectively). This confirmed that the fit of the RLQ ordination sufficiently represented the structures inherent in the three separate tables (Table 5.3).

Table 5.3 Summary results of RLQ analysis (R = sites x environmental variables table; L = sites x species abundance table; Q = traits x species table). R/RLQ(Var) and Q/RLQ(Var) are the variance of environmental and functional trait variables computed for the first two RLQ axes. The covariance and correlation between them are also included.

		RLQ Axis 1	**RLQ Axis 2**
RLQ Summary (% explained variance)			
	R (CA)	93.1	81.4
	L (PCA)	56.3	31.8
	Q (Hill-Smith)	57.5	79.2
	Eigenvalue	67.3	13.1
RLQ analysis	Eigenvalue	0.72	0.14
	Covariance	0.85	0.36
	Correlation: L	0.41	0.21
	R/RLQ (Var)	1.63	1.18
	Q/RLQ (Var)	1.24	1.53

5.4.2 Scale of landscape variables filters movement traits

The results of the fourth-corner analysis yielded eight significant movement trait-environment correlations (step 2, Fig.5.1). The significant correlations corresponded to two movement groups; nomadic birds and inter-African migrants (Fig. 5.2). Migrants were positively correlated with water temperature, rainfall at all lag periods, and the proportion of natural vegetation surrounding a count site. In contrast nomadic birds were negatively correlated with rainfall at all lag periods.

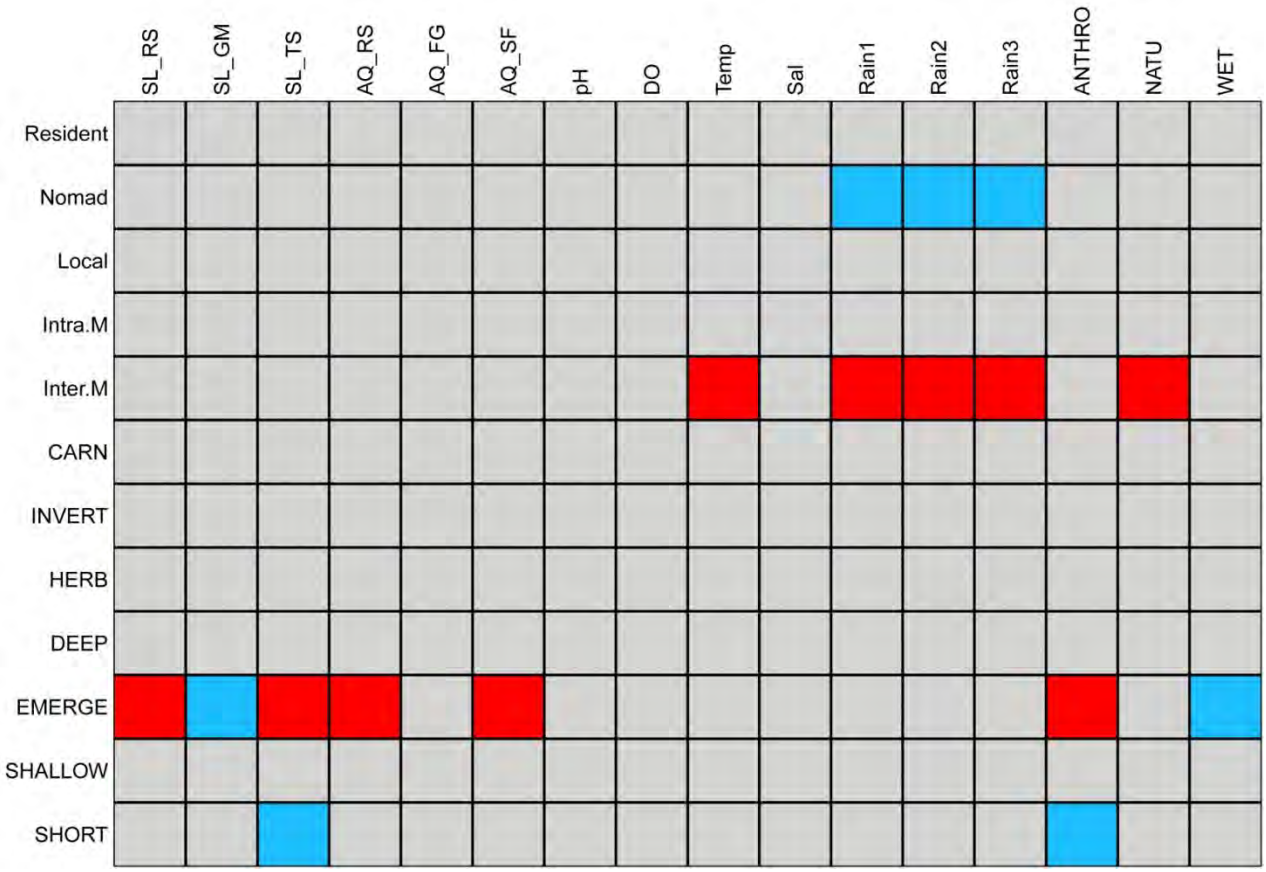


Figure 5.2 Results of the bivariate fourth-corner tests showing the relationship between environmental variables and waterbird functional traits. Significant ($p < 0.05$) positive associations are represented by red cells and significant negative associations are blue cells. P-values were adjusted for multiple comparisons using FDR (false discovery rate) procedure. See Tables 5.1 and 5.2 for description of environmental and trait codes.

5.4.3 Diet and foraging trait association

The fourth-corner results also showed that environmental variables do not only filter movement traits in isolation, but emerge in conjunction with foraging traits (step 2, Fig.5.1). This yielded an additional 11 significant trait-environment relationships (Fig. 5.2). Emergent vegetation foragers had the highest number of significant correlations and showed positive relationships with the proportion of shoreline reeds, sedges, trees and shrubs (Fig. 5.2). They were negatively correlated to the proportion of shoreline grass and mudflats. Emergent foragers correlated positively with the proportion of human modified land cover in the buffer surrounding the count site and smaller wetlands (Fig. 5.2). Short vegetation forager numbers were negatively correlated to the proportion of trees and shrubs surrounding a wetland and well as the proportion of human modified landscapes (Fig. 5.2).

5.4.4 Functional trait clusters and ecological niches

The results of the combined multivariate ordination and fourth-corner RLQ analysis revealed that movement traits and other traits did cluster with habitat characteristics to form ecological niches (step 3, Fig. 5.1). Within the RLQ ordination of environmental gradients (Fig. 5.3), three primary clusters emerged: (1) water quality measurements (pH, salinity and dissolved oxygen) and the proportion of wetland coverage in the buffer were positively correlated with each other; (2) rainfall, proportion of natural vegetation cover in the buffer and shorelines with flooded grass and open shoreline correlated positively; and (3) the proportion of anthropogenic land cover and shoreline & aquatic vegetation (in the form of reeds, emergent and floating vegetation) grouped together and were negatively correlated with the first axis. This created a gradient on the first axis, from left to right, of small, well vegetated wetlands, surrounded by landscapes of high human impact to larger wetlands surrounded by natural vegetation with high salinities and pH and shorelines that consist of short flooded vegetation or mudflats.

The RLQ ordination of functional traits showed a strong influence of emergent and short vegetation foragers, as well as a distinct separation between inter-African migrants and resident species (Fig. 5.4). Birds with a carnivorous diet grouped together with residents and local movers, while migrant and invertebrate feeders which forage in short vegetation were positively correlated. Intra-African migrants and nomadic birds clustered tightly with deep and shallow water foraging traits.

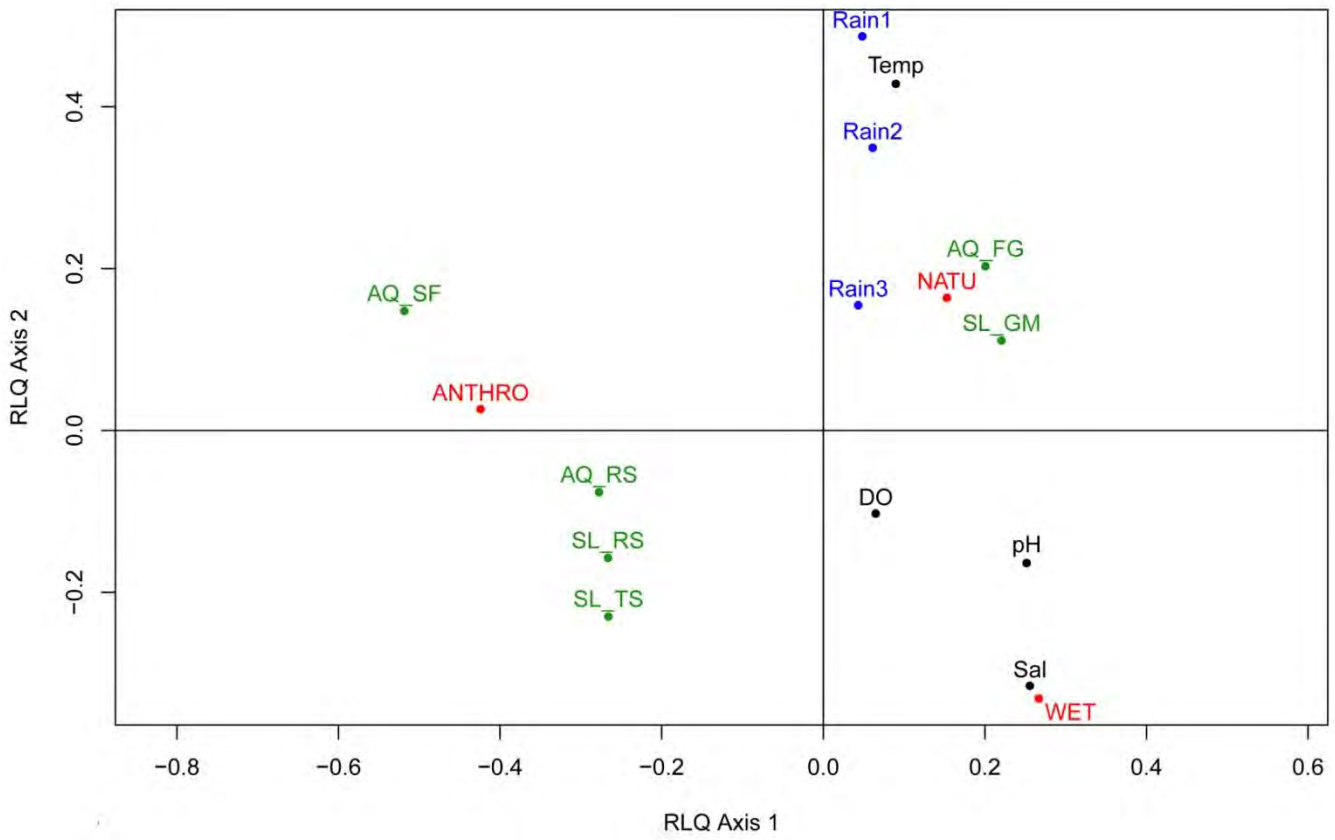


Figure 5.3 Environmental variable RLQ scores along the first two axes. Label colour denotes variable group (red = land cover, blue = rainfall, green = vegetation structure, black = water quality). Similar positions of variables relative to the origin indicate close associations. See Table 5.1 for variable abbreviations.

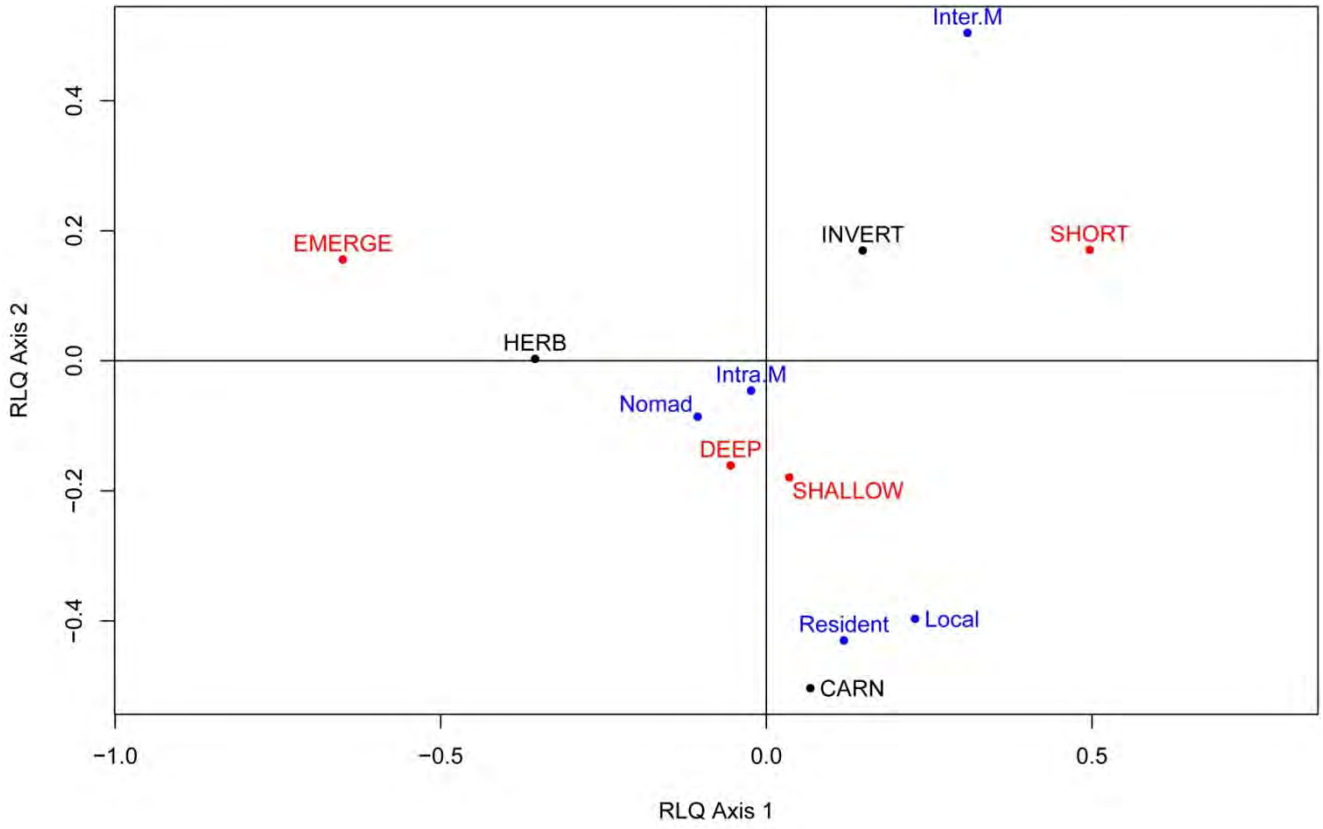


Figure 5.4 RLQ scores along the first two axes for waterbird functional traits. Label colour denotes trait group (red = foraging, blue = movement, black = diet). Similar positions of traits relative to the origin indicate close associations. See Table 5.2 for trait abbreviations

The dotplots of Pearson's correlation coefficient, which indicated the strength and significance of each environmental variable or functional trait against the appropriate RLQ axes, confirmed these patterns (Figs. 5.5 & 5.6). Short vegetation feeders were significantly positively correlated with the first axis, while emergent vegetation foragers where significantly correlated with the first axis (Fig. 5.5a). Associated with these two functional groups were several significant environmental variables. Proportion of wetland and natural vegetation cover, along with flooded and short grass, pH and salinity were significantly positively correlated with the first RLQ axis (Fig. 5.5b). Emergent vegetation foragers were negatively correlated with the first axis along with several environmental variables such as proportion of anthropogenic land cover and proportion of shoreline and aquatic vegetation (Fig. 5.5b). Inter-African migrants were positively correlated to the second RLQ axis (Fig. 5.6a), which corresponded to the pattern of positive correlations of rainfall and water temperature on the second RLQ axis (Fig. 5.6b). In contrast, local movers, residents and carnivorous birds were significantly negatively correlated (Fig. 5.6a). These results showed that along the second RLQ axis there was a clear separation between birds that move at broad scales and those which move at small spatial scales. There were distinctive gradients of separation of movement groups, feeding and dietary traits associated with gradients in the environmental variables, suggesting that birds with different movement abilities occupied different ecological niches. A summary of the findings presented above can be visualised by a RLQ biplot of environmental variables and functional traits (Fig. 5.7)

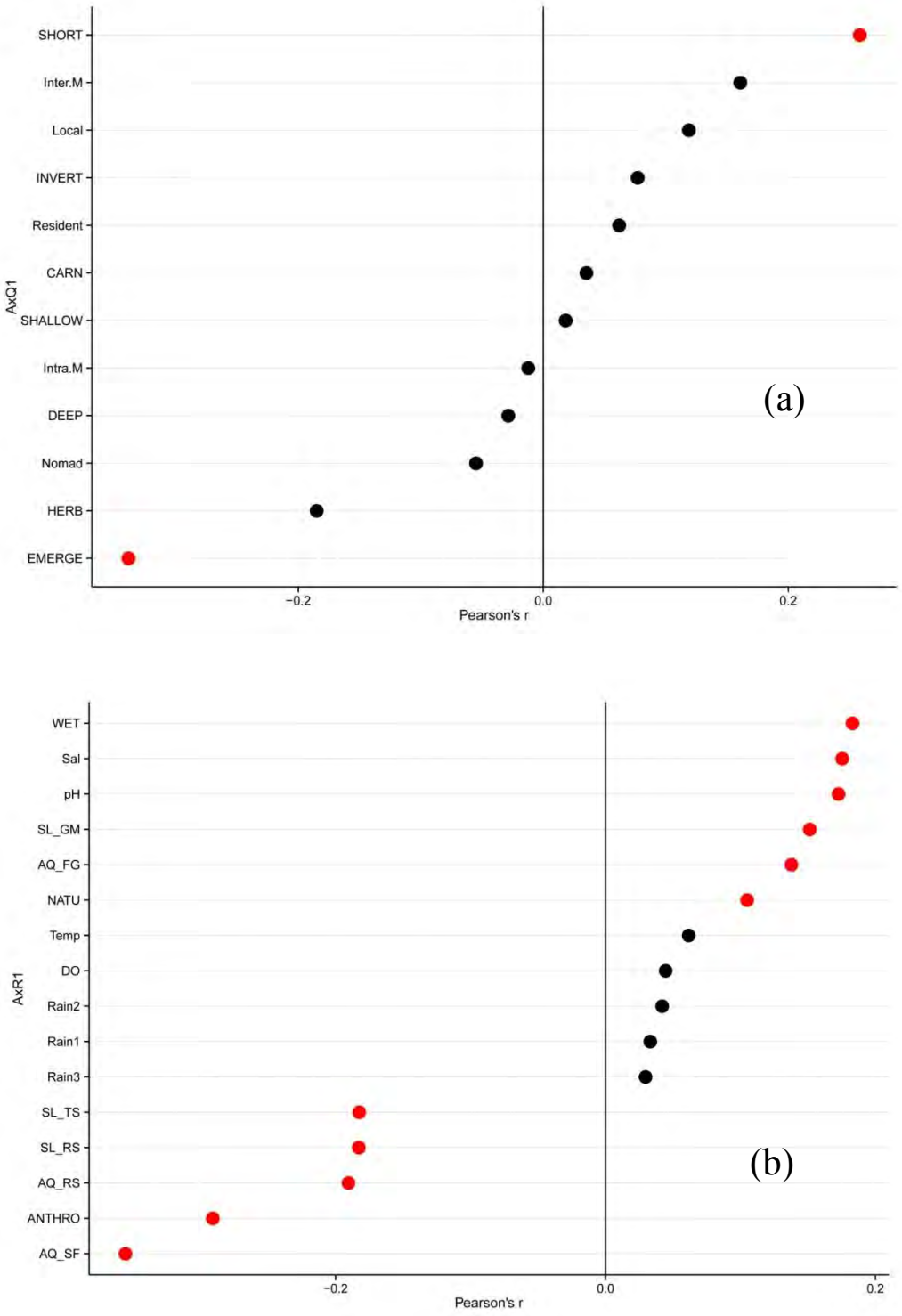


Figure 5.5 Dotplots of Pearson's correlation coefficient derived from the fourth-corner tests applied to the first RLQ axis and (a) waterbird functional traits and (b) environmental variables. Red circles indicate significant correlations ($p < 0.05$).

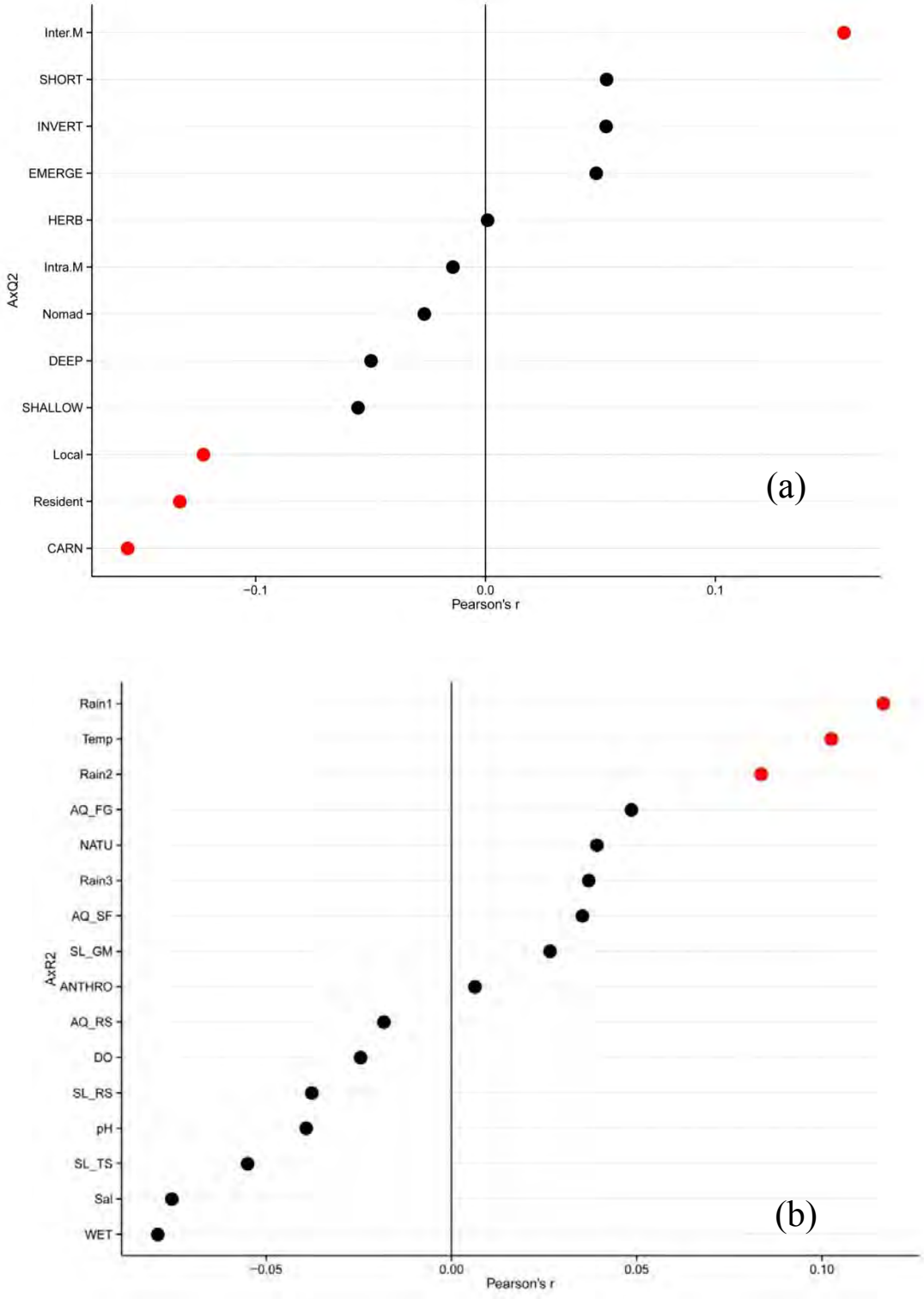


Figure 5.6 Dotplots of Pearson's correlation coefficient derived from the fourth-corner tests applied to the second RLQ axis and (a) waterbird functional traits and (b) environmental variables. Red circles indicate significant correlations ($p < 0.05$).

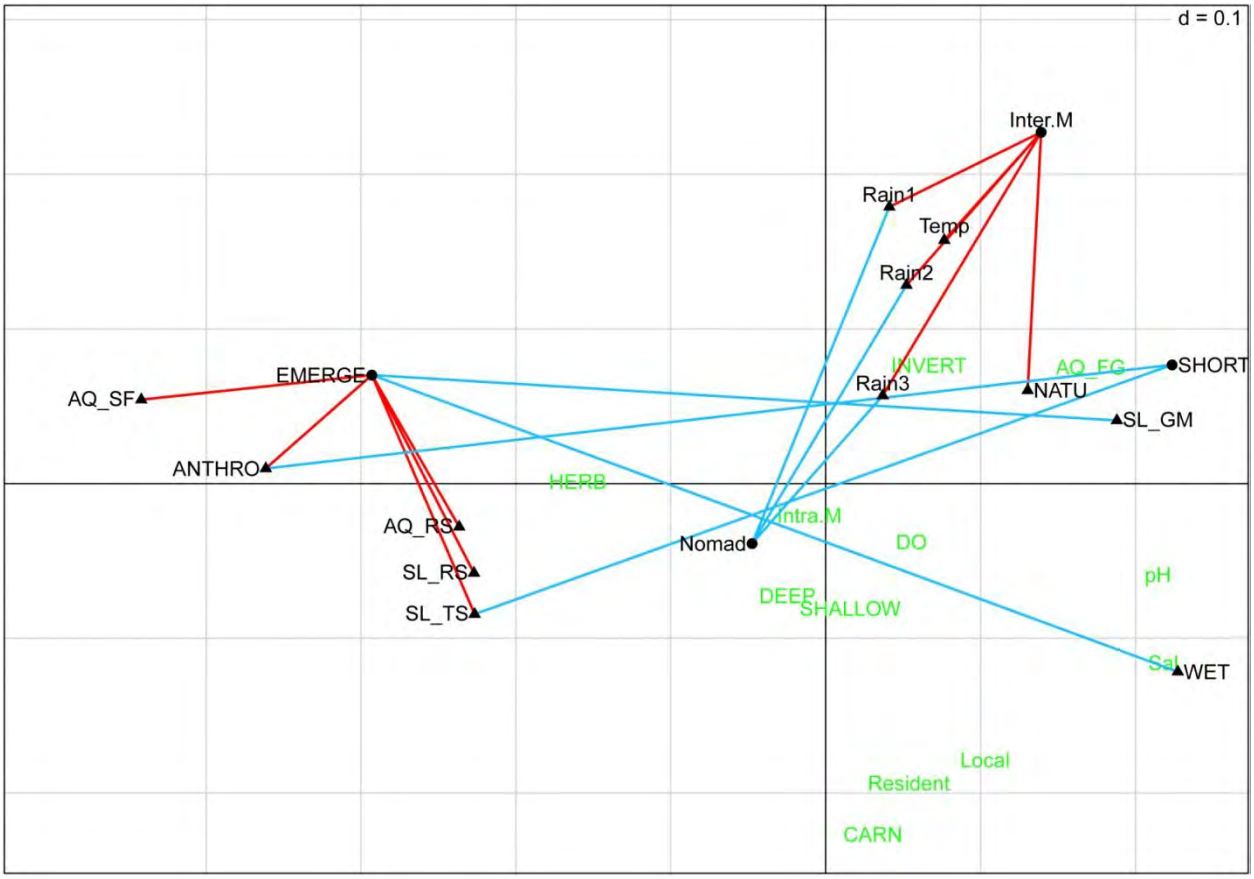


Figure 5.7 Biplot of the combination of RLQ and fourth-corner results showing the relationship between environmental variables and functional traits of waterbirds. Significant ($p < 0.05$) positive associations are represented by red lines and significant negative associations by blue lines. Functional traits are represented by circles, while environmental variables are triangles. Green labels indicate variables that have no significant associations in the fourth-corner analysis. P-values were adjusted for multiple comparisons using FDR (false discovery rate) procedure. See Tables 5.1 and 5.2 for description of environmental and trait codes.

5.5 Discussion

The results of the RLQ and fourth-corner analyses showed that the functional traits of waterbirds are indeed linked to the environmental and habitat characteristics of wetland sites in KwaZulu-Natal, South Africa. The bivariate fourth-corner correlations provided support for the hypothesis that the spatial scale of variation in environmental variables filters traits relating to the ability of waterbirds to integrate differently over variation in landscape resources. Migrants and nomadic waterbirds, both of which have high movement ability, responded to broad-scale variation in land cover and rainfall, although in contrasting ways. Migrants were positively correlated with rainfall at all lag periods and this response was strongest at a one month lag.

In semi-arid regions, rainfall is the primary driver of habitat availability for waterbirds (Kingsford et al. 2010). Throughout most of South Africa, rainfall is generally higher in summer than in winter months, although the extent and amount of precipitation is highly variable in both space and time (Siegfried 1970). Palearctic migrant species in my study sites spend their non-breeding periods in the summer months of South Africa, so the correlation between rainfall and migrant abundance can be partially attributed to a seasonal effect. However, within my study site, spatial variation in rainfall is high (Table 2.5) and the fact that migrants were in higher abundance in wetter parts of the landscape shows that they are still able to respond to broad-scale environmental variation. On the other hand, the abundance of nomads was negatively correlated with rainfall. Summer is the primary breeding period for many resident waterbirds, and many species can breed in small, isolated ephemeral wetlands (Hockey et al. 2005). The majority of censuses were performed at perennial wetland sites, although water levels did show significant fluctuations. This means the potential to detect nomadic species during the breeding season was low. However, a higher abundance of nomads during the dry winter months could indicate that nomads are using coastal wetlands as refuges during the non-breeding season in a similar way to that of altitudinal migrants, which leave the dry interior of South Africa during winter (Johnson and Maclean 1994). As with migrants, this demonstrates that birds which have the ability to move greater distances are able to respond to broad-scale variation in rainfall.

Inter-African migrants were also more abundant at wetland sites surrounded by a high proportion of natural vegetation as opposed to anthropogenically modified land cover. This suggests that migrants may be more sensitive to areas in which anthropogenic disturbance is high, and response to broad-scale land cover patterns might be a way in which to avoid the negative consequences of disturbance. Waterbirds are particularly vulnerable to disturbance and there is evidence that migrant shorebird populations have declined in response to human disturbance (Burger 1986, Pfister et al. 1992, Yasué 2006). Coupled with the decline of many migrant species populations due to other causes, this suggests that the distribution of anthropogenic land cover can negatively affect waterbird conservation efforts. In South Africa, Child et al. (2009) have shown that avian functional groups varied in their response to the amount of agricultural land cover. Grazing birds showed a positive association with agricultural landscapes, which is consistent with my findings that herbivorous waterbirds were associated with an increase in the proportion of anthropogenically modified habitat. This is particularly evident in many duck species (e.g. Egyptian Goose and Red-billed Teal) which use agricultural pastures for feeding and comfort activities (Hockey et al. 2005).

The fourth-corner analysis also revealed strong associations between foraging traits and vegetation structure. This was particularly evident in emergent vegetation foragers and short vegetation (including mudflats) foragers. Emergent vegetation foragers showed a positive correlation with wetland sites that had high proportions of structural vegetation on both the shoreline and within the water column (including reeds, shrubs and trees, emergent, floating and submerged vegetation). Short vegetation foragers did not show any significantly positive relationships to vegetation structure but they were negatively correlated with the proportion of shoreline trees and shrubs. The abundance and type of vegetation has a variety of direct effects on food quantity and water quality available for waterbirds, as well as providing protective cover (Kaminski and Prince 1981, Murkin et al. 1997). The presence of macrophyte vegetation is an important component of wetland habitats, and has been shown to affect waterbird distribution and habitat use (Russell et al. 2009, Terörde and Turpie 2013). Vegetation also has indirect effects in that it can determine the quantity and diversity of substrates for potential prey items such as fish and invertebrates (Balcombe et al. 2005, Hornung and Foote 2006). My results suggest that vegetation structure is a particularly important driver for the distribution of species such as African Jacana, Black Crake, Common Moorhen and African Purple Swamphen. Waterbirds in southern Africa experiencing range

contractions and population decreases are especially reliant on natural vegetation (such as reed beds and floodplains) for breeding (Okes et al. 2008). This underscores that fact that suitable vegetation structure is not only important for foraging activities, but also for successful reproduction.

Land cover surrounding wetland sites was also an important environmental characteristic driving the abundance of emergent vegetation foragers. They were associated with smaller wetlands surrounded by a high proportion of anthropogenic habitat. Two factors might offer an explanation for the emergence of this pattern. Firstly, it is possible that these species are less susceptible to the effects of human disturbance and were thus able to persist in human-impacted habitats. Species within the emergent foraging group (Appendix 1) are small bodied and generally forage singly or in small groups (Hockey et al. 2005). Compared to large bodied and gregarious species these two attributes make them less susceptible to disturbance (Rodgers and Schwikert 2002, Stankowich and Blumstein 2005). Secondly, wetlands in close proximity to agricultural land are often affected by excess nutrient runoff leading to eutrophication events (Hill 2003, Sarneel et al. 2010). Eutrophication events can stimulate the growth of floating macrophyte vegetation (Coetzee and Hill 2012), which in turn increases the amount of habitat available to emergent vegetation foragers. The Mtubatuba and Pongola floodplains clusters are examples for which this is particularly relevant. Both clusters had high numbers of emergent foragers associated with eutrophic water that was impacted by anthropogenic activities. Mtubatuba wetlands were located within a matrix of sugarcane farms, while Pongola sites were located downstream of a large man-made impoundment. The effect of damming upstream of wetland sites has contributed to a marked change in hydrological patterns and mineral composition in these wetlands (Heath and Plater 2010). These changes have increased the nutrient load and at certain periods stimulated extensive surface macrophyte growth in the Pongola sites (Heath and Plater 2010). Such changes in wetland habitats clearly favor species possessing certain functional traits, such as emergent vegetation foragers in this case.

The bivariate test allowed us to address the question of single trait-environment relationships. However, combining the RLQ and fourth-corner analyses in multivariate ordination space provided insight into the covariation of both traits and environmental variables themselves and the co-structure between them. On this basis it was possible to assess the ecological niches of waterbirds with different movement abilities. There was a clear gradient and separation of movement traits into three groups along the second RLQ axis

(Fig. 5.4): (1) residents and local movers grouped together along the negative side of the axis; (2) intra-African migrants and nomads clustered together around the origin; and (3) inter-African migrants were positively correlated with the second axis and strongly opposed the other two movement groups.

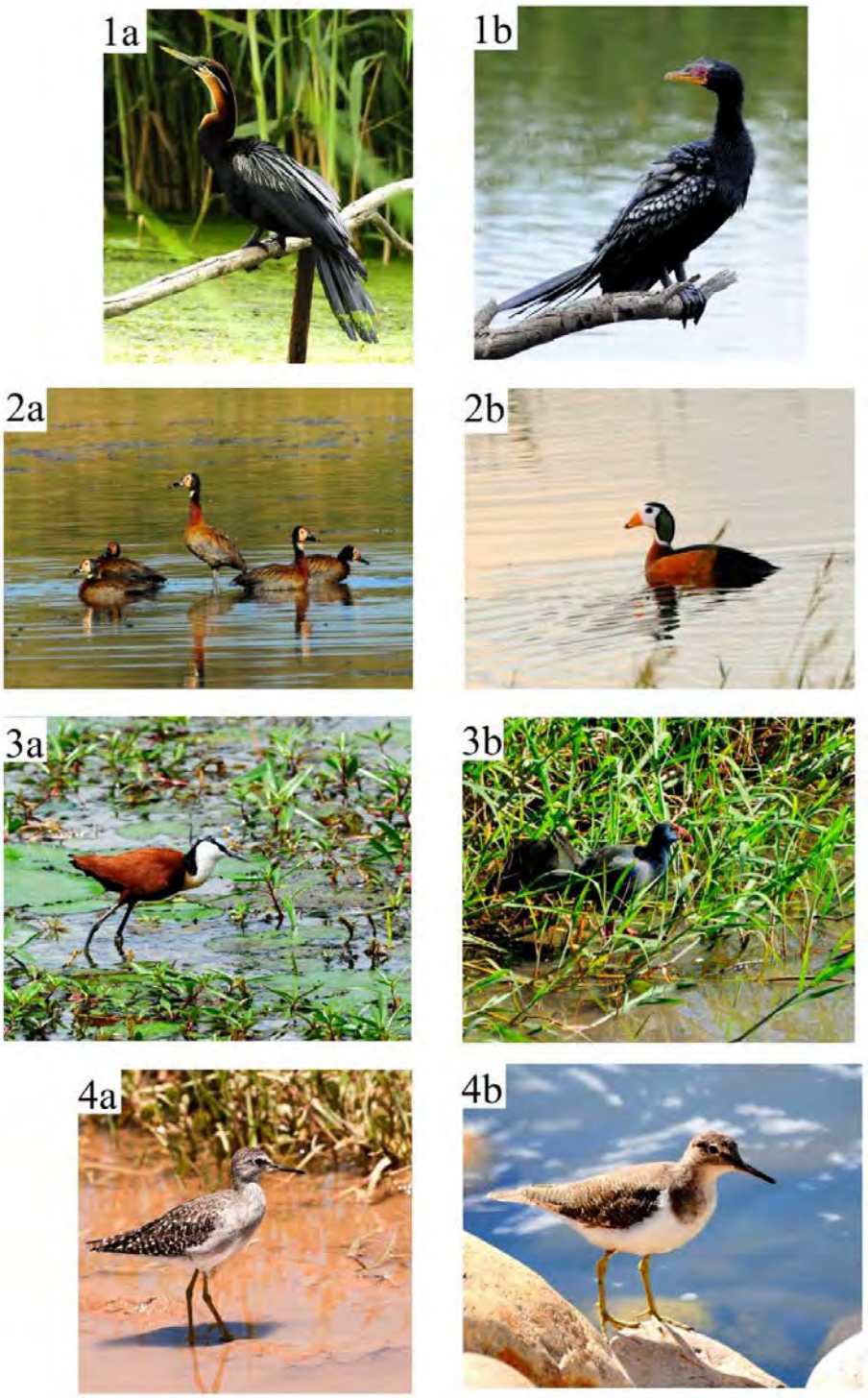
By considering foraging and dietary traits in conjunction with movement traits, there was further evidence for clustering of species exhibiting the following traits: species which were inter-African migrants also fed on invertebrates and foraged in short vegetation and mudflats (Group 1); nomads and intra-African migrants fed in both shallow and deep water (Group 2); and resident and local movers had a carnivorous diet (Group 3). After identifying these groups I could gain insight into their ecological niches by inspecting the environmental variable ordination and identify which specific habitat characteristics co-varied with the groups. The most distinct pattern related to species in Group 1, that were associated with wetlands in which rainfall in lag periods was high and which contained a high proportion of flooded grass, short vegetation and mudflats which were surrounded by high proportions of natural vegetation in the land cover buffer. Group 3 species were more abundant in large wetlands with high salinities and pH. Evidence for a distinct trait grouping-environment relationship was lacking for Group 2, and it appeared that their traits were filtered by intermediate levels of environmental gradients. In the ordination of species scores, all inter-African migrants (e.g., Common Greenshank, Little Stint, Curlew Sandpiper and Ruff) grouped tightly together and this provided further evidence of niche separation from birds within other movement groups. Interestingly, resident small-bodied waders (e.g. White-fronted Plover, Kittlitz's Plover and Three-banded Plover), which share several ecological similarities, did not cluster with migrant waders, providing further evidence that movement strategy played a big role in trait grouping separation.

In a recent review of Palearctic passerines over-wintering in Afrotropical landscapes, Salewski and Jones (2006) concluded that very few generalisations can be made about the ecology of these migrants with respect to habitat use, foraging and social interactions. No such review for Palearctic waterbirds exists, but ideas within Salewski and Jones (2006) do offer avenues through which to explore the question of how residents coexist with migrants on their non-breeding grounds. Migrant species are often more abundant than their resident counterparts and it is assumed that the annual influx of millions of migrants must exert a considerable influence on the ecology and dynamics of resident and nomadic communities. In this respect competition may play an important role. Salewski et al. (2003)

outlined a set of possible scenarios in which migrants have integrated into landscapes occupied by residents, and posited that stochastic events and other factors including interspecific competition form part of the most likely explanation. Although evidence for competitive interactions has been questioned (Salewski and Jones 2006), past competition may have played an important role in driving niche separation, resulting in the evolution of communities that at present do not compete (Salewski et al. 2003, Boyle et al. 2011). This niche separation needs to be put into the context of the divergent goals of residents and migrants. On the wintering grounds migrants are released from the specific habitat requirements needed for breeding, and their fundamental requirements relate to survival in the form of adequate energy intake and escape from predation (Pérez-Tris and Tellería 2002). Indeed, habitat conditions and survival on the non-breeding grounds have important implications for the maintenance of migrant populations, and declines in certain populations have been attributed to conditions outside of breeding areas (Sanderson et al. 2006, Morrison et al. 2013). On the other hand, residents and nomads need to inhabit areas that provide adequate breeding resources. The extent of areas which simultaneously provide waterbirds with both suitable breeding and maintenance habitat may be limited or segregated. In this case, as migrants and resident birds are at different life stages and require different resources, niche separation could occur without extensive competition (Pérez-Tris and Tellería 2002).

The navigational and movement capacities of migrants mean that they are able to respond to broad-scale changes in habitat resources, such as those induced by climate change (Piersma and Lindström 2004, Austin and Rehfisch 2005, Winkler et al. 2014). Certain migrant species may possess the ability to explore novel habitats on a broad scale more quickly but at the expense of detailed knowledge. In contrast, residents may have a more fine-scale, detailed and intimate knowledge of the landscape which they occupy year-round (Mettke-Hofmann and Gwinner 2004). This movement behaviour can provide a great advantage to birds moving at broad scales, and might result in a more temporally flexible use of foraging habitat. This is particularly relevant for birds moving thousands of kilometres that in some instances have very limited knowledge of current environmental conditions on the wintering grounds (Salewski and Jones 2006). A high capacity for adaptation should be present in species that are resilient to climate and anthropogenic change, but paradoxically there are signs that these populations are particularly at risk (Sanderson et al. 2006, Both et al. 2010).

Movement capacity can serve as a mechanism which allows waterbirds to integrate differently over environmental variability, which can itself drive differences in the use of ecological niches. I found support for the hypothesis that highly mobile waterbirds were able to exploit and respond to resources at broader spatial scales than less mobile birds. Employing a functional trait approach allowed us to reveal the factors that structure complex waterbird communities, and I have shown both that the scale of landscape resources can act as a filter on movement traits and that in conjunction with dietary and foraging traits, different movement groups occupy distinct ecological niches. This study provides a framework from which future research into understanding the role of functional traits in structuring communities can be directed and illustrates the utility of RLQ and fourth-corner analyses. I conclude that movement plays a significant role in determining how waterbirds respond to resource dynamics in the southern African landscape, and that the co-existence of migratory and resident birds can partially be attributed to differences in their ecological niches.



Examples of waterbird species in four functional trait classifications: resident, carnivorous and deep water foragers, e.g., African Darter **(1a)** and Reed Cormorant **(1b)**; nomadic, herbivorous and shallow water foragers, e.g., White-faced Duck **(2a)** and Pygmy Goose **(2b)**; nomadic, invertebrate and emergent vegetation foragers, e.g., African Jacana **(3a)** and African-purple Swamphen **(3b)**; and inter-African migrant, invertebrate diet, short vegetation and mudflat foragers, e.g., Wood Sandpiper **(4a)** and Common Sandpiper **(4b)**. Photos: Dominic Henry

5.6 Appendix

Appendix 1. Movement, diet and foraging functional traits of 53 waterbird species used in the RLQ and fourth-corner analysis. See Table 5.2 for trait codes and derivations. Note that a species can exhibit multiple traits within each group. Species classifications are based on those of Hockey et al. (2005) and Okes et al. (2008).

Common name	Latin name	Resident	Nomad	Local	Intra.M	Inter.M	CARN	INVERT	HERB	DEEP	EMERGE	SHALLOW	SHORT
African Darter	*Anhinga rufa*	1	1	1	0	0	1	0	0	1	0	0	0
African Fish-Eagle	*Haliaeetus vocifer*	1	0	1	0	0	1	0	0	1	0	0	0
African Jacana	*Actophilornis africanus*	0	1	0	0	0	0	1	0	0	1	0	0
African Purple Swamphen	*Porphyrio madagascariensis*	1	0	1	0	0	1	1	1	0	1	0	0
African Pygmy-Goose	*Nettapus auritus*	0	0	1	0	0	0	0	1	0	0	1	0
African Sacred Ibis	*Threskiornis aethiopicus*	1	1	1	0	0	1	1	1	0	0	0	1
African Spoonbill	*Platalea alba*	0	1	0	0	0	1	1	0	0	0	1	0
African Wattled Lapwing	*Vanellus senegallus*	1	1	1	0	0	0	1	1	0	0	0	1
Black Crake	*Amaurornis flavirostris*	1	0	1	0	0	1	1	1	0	1	0	0
Blacksmith Lapwing	*Vanellus armatus*	1	1	1	0	0	0	1	0	0	0	0	1
Black-winged Stilt	*Himantopus himantopus*	0	1	1	0	0	1	1	0	0	0	0	1
Cape Shoveler	*Anas smithii*	1	1	0	1	0	0	1	1	0	0	1	0

Common name	Latin name	Resident	Nomad	Local	Intra.M	Inter.M	CARN	INVERT	HERB	DEEP	EMERGE	SHALLOW	SHORT
Caspian Tern	*Sterna caspia*	1	1	1	0	0	1	0	0	0	0	1	0
Cattle Egret	*Bubulcus ibis*	1	1	0	0	0	0	1	0	0	0	0	1
Common Greenshank	*Tringa nebularia*	0	0	0	0	1	0	1	0	0	0	0	1
Common Moorhen	*Gallinula chloropus*	1	0	1	0	0	1	1	1	0	1	0	0
Common Sandpiper	*Actitis hypoleucos*	0	0	0	0	1	0	1	0	0	0	0	1
Curlew Sandpiper	*Calidris ferruginea*	0	0	0	0	1	0	1	0	0	0	0	1
Egyptian Goose	*Alopochen aegyptiaca*	1	1	1	0	0	0	0	1	0	0	0	1
Glossy Ibis	*Plegadis falcinellus*	1	1	1	0	0	0	1	0	0	0	0	1
Goliath Heron	*Ardea goliath*	1	0	1	0	0	1	1	0	0	0	1	0
Great Egret	*Egretta alba*	0	1	0	0	0	1	1	0	0	0	1	0
Great White Pelican	*Pelecanus onocrotalus*	1	1	1	0	0	1	0	0	0	0	1	0
Greater Flamingo	*Phoenicopterus ruber*	0	1	0	0	0	0	1	0	0	0	1	0
Grey Heron	*Ardea cinerea*	1	0	1	0	0	1	1	0	0	0	1	0
Grey-headed Gull	*Larus cirrocephalus*	1	0	1	0	0	1	1	0	0	0	1	0
Hottentot Teal	*Anas hottentota*	1	1	0	1	0	0	1	1	0	0	1	0
Kittlitzs Plover	*Charadrius pecuarius*	1	1	1	0	0	0	1	0	0	0	0	1
Little Egret	*Egretta garzetta*	1	1	0	0	0	1	0	0	0	0	1	0
Little Grebe	*Tachybaptus ruficollis*	1	1	1	0	0	1	1	0	0	0	1	0
Little Stint	*Calidris minuta*	0	0	0	0	1	0	1	0	0	0	0	1

Common name	Latin name	Resident	Nomad	Local	Intra.M	Inter.M	CARN	INVERT	HERB	DEEP	EMERGE	SHALLOW	SHORT
Malachite Kingfisher	*Alcedo cristata*	1	0	0	0	0	1	1	0	0	0	1	0
Pied Kingfisher	*Ceryle rudis*	1	0	1	0	0	1	1	0	0	0	1	0
Pink-backed Pelican	*Pelecanus rufescens*	1	1	0	0	0	1	0	0	0	0	1	0
Purple Heron	*Ardea purpurea*	1	1	0	0	0	1	1	0	0	0	1	0
Red-billed Teal	*Anas erythrorhyncha*	0	1	0	0	0	0	1	1	0	0	1	0
Red-knobbed Coot	*Fulica cristata*	1	1	1	0	0	0	0	1	0	0	1	0
Reed Cormorant	*Phalacrocorax africanus*	1	0	1	0	0	1	0	0	1	0	0	0
Ruff	*Philomachus pugnax*	0	0	0	0	1	0	1	0	0	0	0	1
Spur winged Goose	*Plectropterus gambensis*	0	1	0	0	0	0	1	1	0	0	0	1
Squacco Heron	*Ardeola ralloides*	1	1	0	0	0	1	1	0	0	1	0	0
Three-banded Plover	*Charadrius tricollaris*	1	0	1	0	0	0	1	0	0	0	0	1
Water thick-knee	*Burhinus vermiculatus*	1	0	1	0	0	0	1	0	0	0	0	1
Whiskered Tern	*Chlidonias hybrida*	1	1	0	1	0	1	0	0	0	0	1	0
White-backed Duck	*Thalassornis leuconotus*	0	1	0	0	0	0	1	1	0	0	1	0
White-breasted Cormorant	*Phalacrocorax carbo*	1	1	0	0	0	1	0	0	1	0	0	0
White-faced Duck	*Dendrocygna viduata*	0	1	0	0	0	0	0	1	0	0	1	0
White-fronted Plover	*Charadrius marginatus*	1	0	1	0	0	0	1	0	0	0	0	1
White-winged Tern	*Chlidonias leucopterus*	0	0	0	0	1	1	0	0	0	0	1	0
Wood Sandpiper	*Tringa glareola*	0	0	0	0	1	0	1	0	0	0	0	1

Common name	Latin name	Resident	Nomad	Local	Intra.M	Inter.M	CARN	INVERT	HERB	DEEP	EMERGE	SHALLOW	SHORT
Yellow-billed Duck	*Anas undulata*	1	1	0	0	0	0	1	1	0	0	1	0
Yellow-billed Egret	*Egretta intermedia*	1	0	1	0	0	1	1	0	0	0	1	0
Yellow-billed Stork	*Mycteria ibis*	1	1	0	1	0	1	1	0	0	0	1	0

6 DO SPATIAL OR ENVIRONMENTAL EFFECTS STRUCTURE WATERBIRD METACOMMUNITIES, AND ARE THE PROCESSES TEMPORALLY STABLE?

6.1 Abstract

Metacommunity theory provides a framework for assessing the role of spatial and environmental processes in structuring ecological communities and places emphasis on the role of dispersal. Four metacommunity paradigms have been proposed: species sorting, patch dynamics, mass effects and a neutral model. A primary aim is to decompose the variance in communities into regional and local dynamics and ascribe it to one of these processes, although they are not always mutually exclusive. Most studies have, however, tested these processes based on data from a single sampling period. There is a scarcity of studies which have focused on avian metacommunities, and consensus on structuring forces in these systems is lacking. Using variance partitioning methods I analysed waterbird community data, collected over seven sampling periods at 60 wetland sites in KwaZulu-Natal South Africa, to understand the role of pure environmental effects, pure spatial effects and spatially structured environmental effects. By comparing results across sampling periods, I investigated the role of temporal variation in community processes. The underlying landscape was characterised by four groups of environmental variables: vegetation structure, water quality, rainfall and land cover. Moran's Eigenvector Maps (MEMs) were used to generate a set of multi-scale spatial predictor variables. My results showed that the spatially structured environmental component was dominant through the sampling periods. Purely spatial and environmental components did contribute a significant proportion of variance, however, the magnitude of each showed considerable temporal variation. Environmental processes were more pronounced in the winter periods while purely spatial processes were augmented in the summer months. Our results suggest that the species sorting and niche dynamics are the primary structuring forces in waterbird communities. The presence of the spatial effects, especially in summer, does however suggest that the niche dynamics do not operate in

isolation, and there is thus a need to incorporate spatial structure into community ecology research.

6.2 Introduction

A central goal in ecology is to understand the processes that control the organisation of communities through space and time. An understanding of the role of spatial processes in communities has received considerable attention (Levin 1992) and has given rise to theories that, for example, advocate species diversity as an outcome of colonisation and extinction events (MacArthur and Wilson 1967). In a similar manner, the advancement of our understanding of metapopulation processes has been driven forward by incorporating ideas of dispersal and its role in maintaining connectivity between isolated populations (Hanski 1998, 1999).

The metacommunity perspective (Leibold et al. 2004) provides a productive avenue for disentangling the importance of various multi-scale mechanisms operating on communities. A metacommunity is a set of local communities that are linked, via dispersal, by an assemblage of potentially interacting species (Wilson 1992). There are four paradigms (species sorting, mass effects, patch dynamics and the neutral model) that form the basis of metacommunity theory. Each advocates a different set of mechanisms by which natural communities are, and have been, shaped (Leibold et al. 2004). A fundamental principle common to all of these paradigms is the ability of organisms to exhibit movement, either within or between local communities. These movements can be a response to competition, tracking of environmental change or other dynamics which lead to either immigration into a habitat patch or emigration from a habitat patch (Leibold et al. 2004, Holyoak et al. 2005). Different paradigms also hold different assumptions about the relative importance of local-scale environmental conditions and spatial processes that operate at broader scales (Leibold et al. 2004). The species sorting paradigm suggests that community composition is driven by environmental characteristics and gradients while the neutral model (Hubbell 2001) assumes that species are not fundamentally different and community composition is thus determined by dispersal and spatially random events. Following this, the neutral model suggests that community dissimilarity should increase as a function of geographical distance. The mass effect perspectives emphasises the role of both local and regional processes on community structure (i.e. a combination of both environmental conditions and dispersal among sites). It

shares similarities with the species-sorting model, but the strength of the niche dynamics is filtered by independent dispersal processes (Leibold et al. 2004). The patch dynamics perspective, which shares characteristics with the neutral model, assumes a high similarity in the quality of habitat patches and so all patches have an equal probability of hosting populations. Community structure in this model is dispersal limited and dominated by extinction and colonisation events (Leibold et al. 2004).

It has recently been acknowledged that these four paradigms are not as discrete as previously thought, and that metacommunities are shaped by a combination of processes (Logue et al. 2011). For example, Winegardner et al. (2012) proposed that mass effects and patch dynamics are actually special cases of the species sorting paradigm. As an alternative to four discrete paradigms, the metacommunity framework can be seen as a continuum along which the species-sorting and neutral models are different endpoints of a set of processes that act on community structure. Viewing communities in this way does, however, pose challenges for empirical studies that seek to test the relative importance of the processes defined by the four paradigms.

Beta-diversity – defined as the variation in species composition among sites within a study region of interest (Whittaker 1962, 1970) – is a central concept in metacommunity theory. Beta-diversity can be generated and maintained by both spatial and non-spatial processes. A primary aim when analyzing beta-diversity is to discriminate between sources of variation and model the relevant sources separately (Legendre et al. 2005). Variance partitioning has become a widely used and powerful approach to disentangle the relative roles of local environmental characteristics and spatial characteristics of observed beta-diversity within a study system (Legendre et al. 2005, Logue et al. 2011). The variance partitioning procedure requires three data sets, namely a community composition matrix (either abundance or presence-absence), a matrix of relevant environmental variables and a matrix representing the spatial configuration of the sampling locations (Cottenie 2005). Variance partitioning then allows for decomposition of beta-diversity into three causal fractional components (Legendre et al. 2005, Peres-Neto et al. 2006): (1) purely spatial (PS, with the effect of environment partialled out); (2) purely environmental (PE, with effect of space partialled out); and (3) spatially structured environmental (SSE, the shared environment-space fraction). Investigating the predominance of each of these components can then be used as a means to inform our understanding of the metacommunity processes underlying the observed beta-diversity patterns. A large proportion of the PS fraction supports the patch

dynamics and neutral model perspective (Hubbell 2001). Conversely, a large proportion the PE fraction lends weight to species sorting and niche-based processes structuring communities (Logue et al. 2011). A large SSE fraction could arise from species sorting processes if the relevant environmental gradients are themselves spatially autocorrelated (Cottenie 2005, Winegardner et al. 2012, Gianuca et al. 2013). A high proportion of both PS and PE provided support for a combination of species sorting and mass effects (Cottenie 2005). Figure 6.1 provides a visual illustration of how the significance and relative contribution of variance of each component indicates a specific metacommunity process.

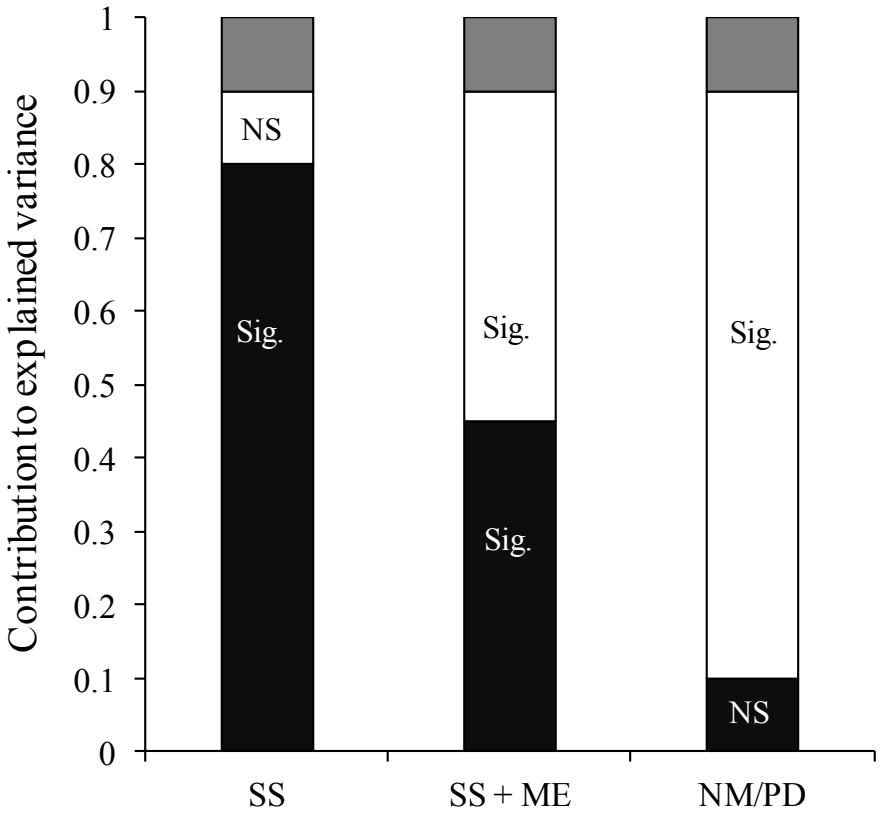


Figure 6.1 A hypothetical illustration of the variance partitioning components, and their relative variance contribution, associated with each metacommunity type. The components are made up of pure environmental fraction (black), pure spatial fraction (white) and spatially structured environmental fraction (grey) and differ in whether they contribute a significant proportion to the overall explained variance in the ecological community. SS, species sorting, ME, mass effects, NM, neutral model, PD, patch dynamics, Sig, significant fraction; NS, non-significant fraction.

Understanding metacommunity processes is not only important from a theoretical perspective, but can also provide a framework for approaching applied conservation strategies such as bioassessment (Heino 2013), biomonitoring (Siqueira et al. 2012) and biodiversity maintenance (Economo 2011, Diaz et al. 2013). These strategies are especially relevant in ecosystems experiencing high levels of habitat fragmentation, which itself can hinder the ability of organisms to disperse between local communities and contribute to species loss (Zartman and Nascimento 2006). It is therefore important to empirically test hypotheses of metacommunities from a multitude of ecological systems to elucidate general patterns (Logue et al. 2011). Avian metacommunities provide an ideal study system because birds generally have high dispersal capacity and are often sensitive to environmental change. In addition there have been very few avian metacommunity studies - in a review of 158 data sets used for the purpose of space-environment variance partitioning (Cottenie 2005) only 3% of studies related to birds. Findings in avian studies have also supported varied metacommunity paradigms; Meynard and Quinn (2008), Gianuca et al. (2013) and Özkan et al. (2013) showed that environmental variables were the predominant drivers of community structure (although at different scales) for their bird communities, while Driscoll and Lindenmayer (2009) found little consistent support for any of the metacommunity theories.

The objective of this analysis was to assess the relative roles and importance of spatial and environmental components in structuring a waterbird metacommunity on the coastal plain of KwaZulu-Natal, South Africa. More specifically, I aimed to distinguish the processes driving beta-diversity across 60 sites in a large network of wetlands and identify which metacommunity perspectives best explained these patterns (e.g. neutral vs species sorting). Environmental variables, which were measured at each site, fell within four classes: vegetation structure, water quality, rainfall and land cover. I used Moran's Eigenvector Maps (MEMs, Dray et al. 2006, 2012) to create and model the spatial component of the wetland system. I addressed two primary questions: (1) what are the relative contributions of the PE, PS and SSE fractions to the total explained variance of the beta-diversity of the waterbird community and how much variation in the waterbird communities can be attributed to stochastic variation; and (2) if PE explains a significant proportion of variance in the communities, which environmental variables were most important in contributing to this explained variance? My study involved repeat sampling (of both waterbird community and environmental characteristics at the same sites) over seven different periods equally spread across 14 months. This allowed me to extend the analysis and investigate the role of temporal

variation in community structuring processes. Each sampling period was analysed to address my two focal questions, after which comparisons were made between findings from different sampling periods to test whether metacommunity processes were temporally stable through a mosaic of wetlands.

6.3 Methods

6.3.1 Study site

The study was undertaken on the coastal plain of KwaZulu-Natal, South Africa. The study sites included 60 wetland sites across 14 wetlands (Chapter 2, Figure 2.3). Sites were grouped according to wetland clusters. See Chapter 2 for full details of study area and wetland clusters.

6.3.2 Waterbird community surveys

Standardised bimonthly point counts at 60 sites across the study area were carried out from April 2012 to June 2013. This resulted in 7 sampling replicates for each of the 60 sites. All counts were carried out within the first 10 days of each sampling month. Details of counting are provided in Chapter 2. See Appendix 1 for a list of waterbird species included in the analysis.

6.3.3 Environmental predictors

Four groups of environmental variables were measured at each site during each sampling period. These were vegetation structure (shoreline and aquatic), water quality, rainfall (at 3 monthly lag periods) and proportion of three land cover classes in a 3 km buffer surrounding each sampling site. See Chapter 2 for derivation and abbreviation for each variable and Tables 2.3 to 2.6 for a summary of environmental variables measurements in each wetland cluster.

6.3.4 Spatial predictors

I used distance-based Moran's eigenvector maps, MEMs (Dray et al. 2006, 2012), representing spatial structures at multiple scales, to generate spatial predictor variables across our network of study wetlands. MEMs are a generalised form of older methods known as

principal coordinates of neighbourhood matrices, PCNM (Borcard and Legendre 2002). PCNM methods, which have been widely applied, produce a set of linearly independent spatial predictor variables (i.e. orthogonal eigenvectors). The first step of the PCNM approach requires the computation of a Euclidean distance matrix between the sampling locations. A threshold value is then chosen (usually the shortest distance which allows all sampling locations to remain connected) and used to construct a truncated version of the distance matrix. Eigenvectors are then extracted after a principal coordinate analysis (PCoA). Positive eigenvectors are then retained as spatial descriptors. The scale of spatial variation, starting at the broadest scale, decreases from the first to the last eigenvector. Dray et al. (2006) built on this method to create MEMs, which incorporate two significant advances. First, instead of using a single truncation distance, the MEM approach allows for connectivity matrices to be defined by several types of neighbourhood networks. Second, connections between each sampling site can be weighted using one of several weighting functions. Combining a connectivity matrix (CM) and a weighting matrix (WM), via the Hadamard product of CM and WM, results in a spatial-weighting matrix (SWM) which represents a customised model of the spatial relationships among sampling locations.

Dray et al. (2006) highlighted the importance of choosing a WM, especially for sampling designs which are irregular in geographical space, as was the case in our study. They suggested that identifying the WM that results in the optimal performance of the spatial model is best done using a data-driven approach. The steps behind the approach include first defining the different combinations of CMs and WMs (based on weighting functions) and then calculating MEMs for each of these combinations and regressing them against the waterbird community data using redundancy analysis (RDA). MEMs with the highest explanatory power are retained and an AIC_c value (Burnham and Anderson 2002) for each model is then calculated. The CM and WM of the model with the lowest AIC_c are then selected for further analysis.

To remove linear effects, waterbird community data were detrended prior to inclusion into the MEM analysis. First, a linear regression between the waterbird community matrix and x-y coordinates of sampling sites was run. If there was an overall significant trend, then the residuals of the regression were used as the values of the community matrix.

I followed this procedure and defined five types of CMs: (1) distance-based criterion (dnn); (2) Delaunay triangulation (del); (3) Gabriel graph (gab); (4) relative neighbourhood

graph (rel) and; (5) minimum spanning tree (mst). An assumption underlying the following weighting functions is that ecological and geographical distances are positively related. Associated with these I defined four weighting functions: (1) binary weighting (i.e. 1 or 0 depending on whether sites are connected or not); (2) linear (f1 = 1- d_{ij}/max(d_{ij})); (3) a concave-down function (f2 =1−(d_{ij}/max(d_{ij}))$^{\alpha}$); and (4) a concave-up function (f3 =1/d_{ij}^{β}). For all functions, d_{ij} is the distance between point *i* and *j*. Following the recommendations of Dray et al. (2006), I considered a sequence of integers ranging from 2 to 10 for both α and β. I then tested each unique combination of the CMs and WMs. This resulted in 20 unique spatially-weighted matrix models entered into the model selection procedure

The dnn approach for defining a CM requires further explanation. In this approach, sites *i* and *j* are considered neighbours if $d_{ij} < \gamma$. To identify the optimal radius, I tested 10 evenly distributed values of γ ranging from $dist_{min}$ to $dist_{max}$. The minimum value, $dist_{min}$, was defined as the minimum distance which ensured all sampling sites remain connected. The maximum value, $dist_{max}$, was determined by inspecting a multivariate variogram of the Hellinger transformed community data. The $dist_{max}$ was the highest distance at which the value of the variogram was significant.

This data-driven approach was applied to community data from each sampling period independently. This resulted in 7 SWMs through which MEMs for each separate mission were calculated (e.g. for the April 2012 sampling period the model with the lowest AIC_c was the result of the dnn CM with the f2 weighting function (WM) with α = 6 and γ = 36.84 km)

6.3.5 Statistical analysis

I used the variance partitioning approach (Borcard et al. 1992, Peres-Neto et al. 2006), applied to data from each sampling period, to address our first question of the relative role of spatial and environmental variables in explaining variation in waterbird beta-diversity. The variance partitioning approach takes three matrices that were structured as follows (rows x columns): waterbird community (60 sites x 53 species), spatial predictors (60 sites x 8 MEMs) and environmental (60 sites x 16 environmental variables). The aim was to partition the variance in the response matrix (waterbird community) by the spatial and environmental matrices using the adjusted R-squared (R^2_{adj}) in RDA. The significance of the unique fraction of R^2_{adj} (while constraining other fractions) for each predictor matrix as well as their

combined fractions was tested for significance using Monte Carlo permutation tests (n = 999). Before implementing the variance partitioning I used forward stepwise selection with a double-stopping criterion (Blanchet et al. 2008) to identify significant spatial and environmental variables, and included only these variables in the variance partitioning analysis as recommended by Peres-Neto and Legendre (2010). The waterbird community data matrices were Hellinger transformed prior to inclusion in the analysis (Legendre and Gallagher 2001).

To address my second question, I used the R^2_{adj} value of environmental variables retained by the forward selection procedure to assess the relative contribution of each environmental variable to the purely environmental component of the variance partitioning output.

All analyses were run in the R statistical software (R Core Team 2013). The spatial predictors were created using functions within the spacemakeR package (Dray 2013), the stepwise selection procedure was run using the packfor package (Dray et al. 2013) and the variance partitioning was carried out using the *varpart* function in the vegan package (Oksanen et al. 2013).

6.4 Results

6.4.1 Spatial weighting matrices and MEMs

The results of the data-driven approach to selecting the most suitable spatial model for each sampling period are shown in Table 6.1. For all sampling periods the best spatial weighting matrix (i.e., the model with the lowest AIC_c) was created using the distance criterion (dnn) connectivity matrix. The corresponding weighting functions selected changed through the sampling periods and included the binary weighting (Oct 2012), linear weighting f1 (Dec 2012) and concave down weighting f2 (Apr 2012, Jun 2012, Feb 2013, Apr 2013, Jun 2013). The α value for f2 functions ranged from 2 to 6, while the γ value ranged from 31.25 to 45.32 km (Table 6.1). The full modelling outputs for spatial weighting matrices selection of each sampling period are presented in Appendix 2. Following the selection of the most suitable spatial weighting matrices, MEM eigenvectors were created for each sampling mission. Using the spatial data from April 2012 as an example, Fig. 6.2a shows how the first MEM

corresponds to broad-scale spatial patterns, while Fig. 6.2b (which is the last positive MEM) shows a correspondence to fine-scale spatial patterns.

Table 6.1 Results of the spatial model with the highest support for each sampling period following the data-driven approach for selecting the appropriate spatial weighting matrix. The distance-based criterion (dnn) was selected as the connectivity matrix in all sampling periods. bin, binary; f1, linear function; f2, concave-down function. The units of the γ parameter are in km. The value of α is one of nine integers ranging from 2 to 10. Appendix 2 contains the full model outputs for each sampling period.

Sampling period	Weighting function	AICc	Parameter values
Apr '12	f2	-18.99	α = 6; γ = 36.84
Jun '12	f2	-21.14	α = 2; γ = 45.32
Oct '12	bin	-19.24	γ = 32.42
Dec '12	f1	-17.44	γ = 44.31
Feb '13	f2	-17.44	α = 4; γ = 31.25
Apr '13	f2	-16.75	α = 3; γ = 39.15
Jun '13	f2	-17.46	α = 2; γ = 40.18

6.4.2 Variance partitioning

The total variance in the waterbird community explained by both spatial and environmental matrices ranged from 15.4 to 24.7% across different sampling periods (Table 6.2). The explained variance was significant ($p < 0.05$) throughout all sampling periods. Interestingly, the lower and upper bounds of this explained variance occurred in June 2013 and June 2012 sampling periods respectively, suggesting marked differences in explanatory power of spatial and environmental variables between years. The purely environmental fraction of explained variance ranged from 3.0 (Oct 2012) to 9.5% (Apr 2013) and all fractions were highly significant ($p < 0.005$) after partialling out the effect of the spatial variables (Table 6.2). The lowest purely environmental fractions occurred during the summer months (3.0, 3.6 and 4.6%). The purely spatial fraction of explained variance ranged from 0.9 (Apr 2013) to 7.9%

(Oct 2012) and all fractions, except that of the Apr 2013 sampling period, were significant after partialling out the effect of environmental variables. The spatially structured environmental fraction (i.e. shared fraction between spatial and environmental variables) ranged from 6.1 (Jun 2013) to 12.8% (Jun 2012). As was the case for total explained variance, the upper and lower bounds of the SSE fraction occurred in the June months of the study period (Table 6.2).

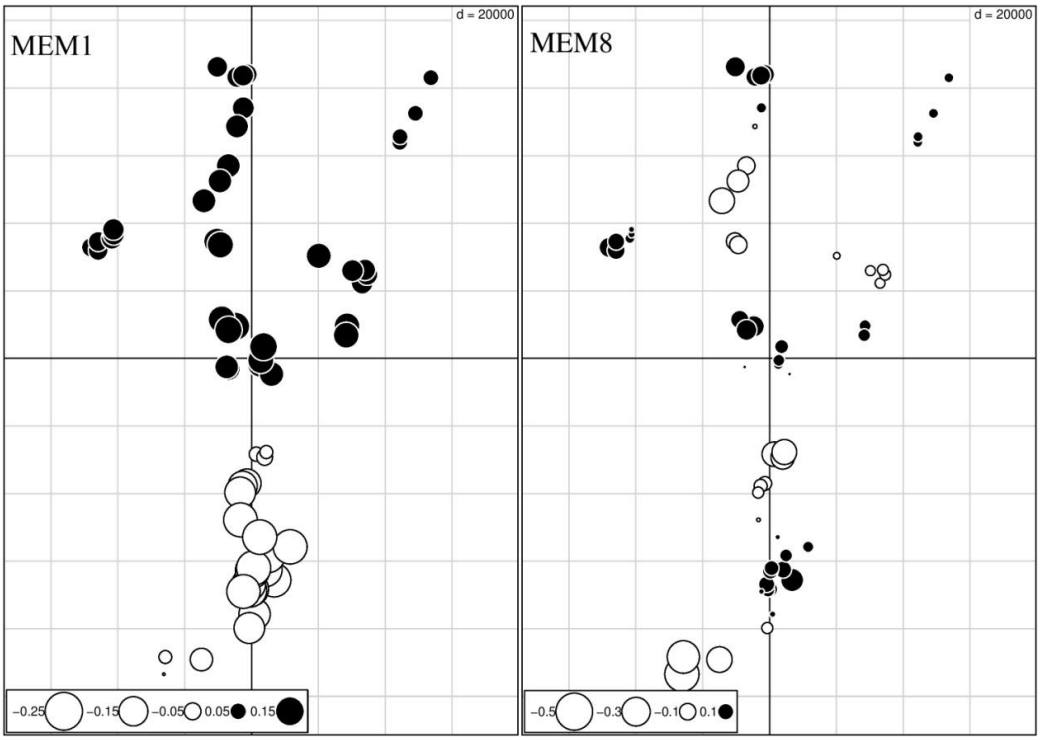


Figure 6.2 Example of two MEMs in geographical space from April 2012. MEMs were used as spatial predictors in the variance partitioning of the waterbird metacommunity. The figure on the left (Fig. 6.2a) is the first MEM which represents broad-scale variation, while the figure in the right (Fig. 6.2b) is the eighth MEM representing fine-scale variation. White and black circles relate to negative and positive values respectively. The size of the circle relates to the magnitude of the eigenvalue. At each scale the MEMs are generated with the aim of maximising their correlation with the scores of the multivariate waterbird community matrix. Points of similar size and colour represent communities that are compositionally similar, while those of different size and colour illustrate dissimilar communities. The grid size, *d,* is measured in meters.

Table 6.2 Summary of the variance partitioning analyses for the waterbird metacommunity showing the percentage of variance contributed by each component (each row is a sampling period). Significance of a fraction, after partialling out other effects, is shown beside the fraction value. PE, pure environmental fraction; PS, pure spatial fraction; SSE, spatially structured environmental fraction (i.e. shared spatial and environmental fraction). Total, sum of explained variance of the three components. NS, non-significant; **, $p < 0.005$; *, $p < 0.05$.

	PE		**PS**		**SSE**	**Total**	
Apr '12	5.6	$F_{6,48} = 1.61$ **	4.1	$F_{5,48} = 1.52$ **	7.8	17.5	$F_{11,48} = 2.14$ **
Jun '12	7.1	$F_{7,42} = 1.66$ **	4.9	$F_{7,42} = 1.45$ **	12.8	24.7	$F_{14,42} = 2.31$ **
Oct '12	3.0	$F_{6,44} = 1.32$ *	7.9	$F_{9,44} = 1.59$ **	10.3	21.2	$F_{15,44} = 2.06$ **
Dec '12	3.6	$F_{6,47} = 1.37$ **	4.5	$F_{6,47} = 1.46$ **	7.9	15.9	$F_{12,47} = 1.93$ **
Feb '13	4.6	$F_{4,48} = 1.74$ **	5.6	$F_{6,48} = 1.62$ **	8.6	18.8	$F_{10,48} = 2.34$ **
Apr '13	9.5	$F_{8,46} = 1.81$ **	0.9	$F_{5,48} = 1.12$ NS	9.8	20.3	$F_{13,48} = 2.15$ **
Jun '13	6.9	$F_{6,48} = 1.73$ **	2.3	$F_{5,48} = 1.29$ *	6.1	15.4	$F_{11,48} = 1.97$ **

The relative contribution of each component (PE, PS and SSE) to the total explained variance is presented in Figure 6.3. The SSE component remained fairly stable throughout the sampling periods (range: 40 to 52%). The PS and PE, however, showed greater differences in magnitude throughout the sampling periods (PS range: 4 to 37%; PE range: 14 to 47%). The April 2013 sampling period was unique in having the lowest PS fraction and highest PE fraction (Fig. 6.3). Again this highlights the prominence of PS fractions in the summer months, while PE fractions are elevated in the winter months, suggesting that there is indeed a seasonal difference in the processes structuring waterbird metacommunities.

For each sampling period several environmental variables (range: 4 to 7) were retained after the stepwise selection procedure and were combined to represent the purely environmental component of the variance partitioning analysis. The relative contribution to variance (measured by R^2_{adj}) is shown for individual variables in Table 6.3, while that of variable groups is shown in Fig. 6.3. For individual variables, salinity and the proportion of emergent, floating and surface aquatic vegetation were consistently retained in all but one sampling period (Oct 2012). All other variables were retained in at least one sampling period model expect for proportion of natural vegetation cover in the buffer surrounding sampling

sites. Vegetation structure consistently contributed the highest proportion of variance to the purely environmental component across all sampling periods and ranged between 38.1 and 60% (Fig. 6.4). Water quality explained the next highest proportions of variance in all sampling periods except for in Oct 2012, where it did not contribute at all. The contribution from rainfall variables varied substantially throughout the study period ranging between 0 and 25%. Land cover variables were only retained in four of the seven sampling periods and displayed a lower contribution of variance ranging from 0 to 22.4% (Fig. 6.4). In general, water quality was more important in the winter months while the effect of land cover was more prominent in the summer months.

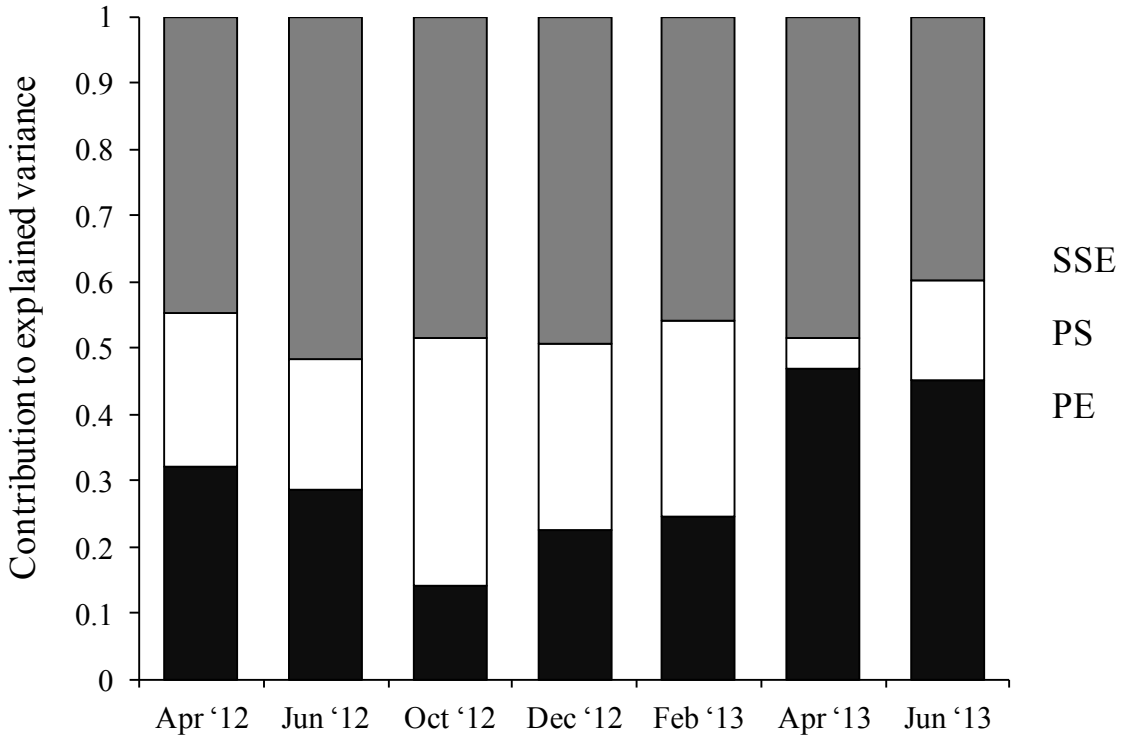


Figure 6.3 The relative contribution of pure environmental fraction (black), pure spatial fraction (white) and spatially structured environmental fraction (grey) to the total explained variance in the variation partitioning procedure for each sampling period.

Table 6.3 Relative contribution (percentage of total) of variance, measured by R^2_{adj}, of each individual environmental variable in the pure environmental component of the variance partitioning. Variables were selected via a forward-stepwise selection procedure. See Table 5.1 for variable abbreviations and derivations.

	SL-RS	**SL-GM**	**SL-TS**	**AQ-RS**	**AQ-FG**	**AQ-SF**	**pH**	**DO**
Apr '12						38.1	16.3	
Jun '12		7.6		11.7	12.0	8.7		
Oct '12	12.5	14.3	11.1					
Dec '12					13.1	29.6	12.4	11.1
Feb '13		15.5				27.0		
Apr '13			7.4		8.3	34.9	7.6	8.3
Jun '13	10.7		14.6			34.6		

	Temp	**Sal**	**Rain1**	**Rain2**	**Rain3**	**ANTHRO**	**NATU**	**WET**
Apr '12		11.8		11	10.8	12.1		
Jun '12		26.2			11.8	22.0		
Oct '12			25.0			22.4		
Dec '12		19.8		14.0				
Feb '13		38.2	19.2					
Apr '13	8.2	18.4						6.8
Jun '13		16.7			11.3			12.0

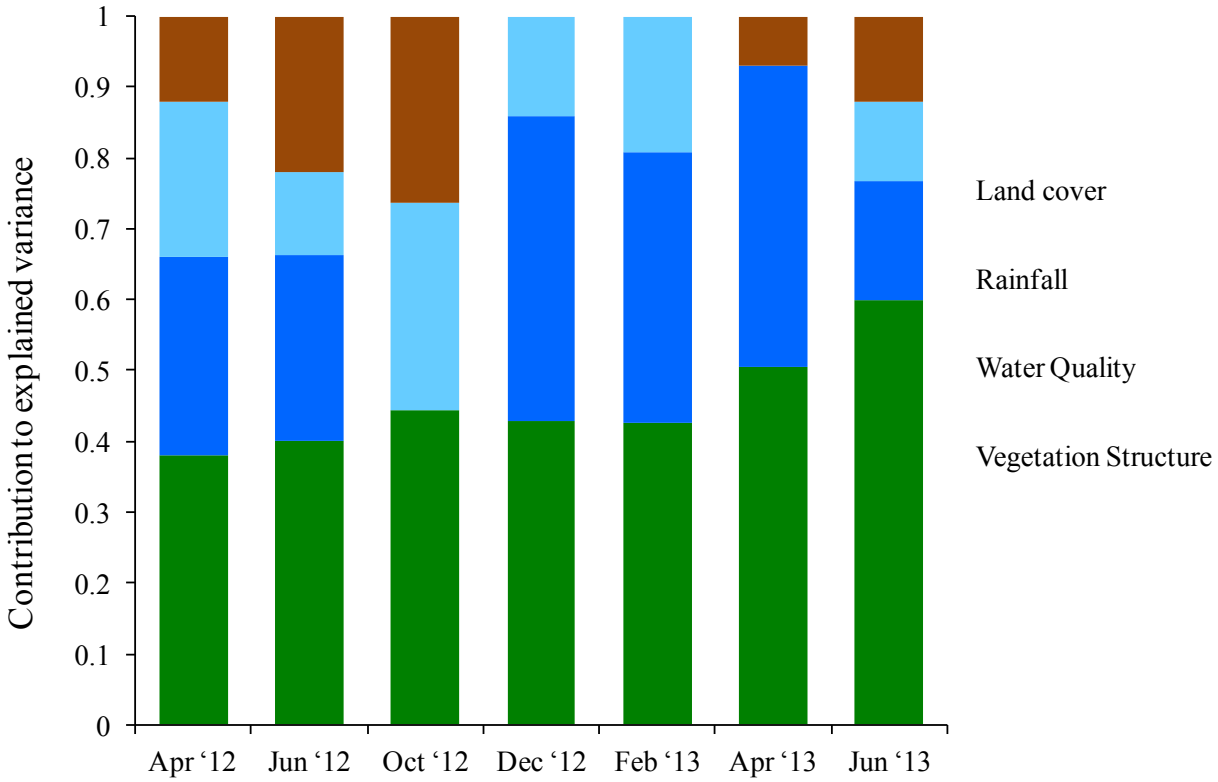


Figure 6.4 The relative contribution of variance (measured by R^2_{adj}) by each group of environmental variables in the pure environmental component of the variance partitioning. Variables were selected via a forward-stepwise selection procedure with a double-stopping criteria. Vegetation structure (green), water quality (blue), rainfall (light blue), land cover (brown).

6.5 Discussion

I used the metacommunity framework to investigate the processes structuring beta-diversity of waterbird communities across a network of wetland sites. The results of the variance partitioning procedure showed that, in general, all three components (PE, PS and SSE) contributed significantly to the overall explained variance in waterbird communities, although the relative importance of each changed through the sampling periods. The SSE fraction, which is the shared fraction between space-environment variables, was the dominant (contributing an average of 47% to explained variance) and most stable component across all but one sampling period (June 2013). The relative contribution of PE and PS fractions

changed through the sampling periods. The PE fraction was consistently larger in winter months (April to September), while PS fraction was consistently larger in the summer months (October to March). Overall the majority of variance explained by the various components included environmental variables. This provides support that species-sorting and niche dynamics are the primary processes structuring the waterbird metacommunity. The presence of a significant purely spatial effect, however, especially during the summer months, indicates that neutral and dispersal dynamics do indeed play a role in metacommunity structure. This result is surprising, given that waterbirds are highly mobile and that my study system lacked any significant barriers to dispersal.

Guidelines for metacommunity analysis have been proposed by Cottenie (2005), who conducted a meta-analysis of the role of space and environment characteristics in metacommunity studies. He compiled 158 data sets across multiple taxa which incorporated various scales of analysis and dispersal modes (Cottenie 2005). Variance partitioning was subsequently used to assign a metacommunity process driving the dynamics of each data set. Cottenie (2005) reasoned that when the total explained variance in beta-diversity is decomposed into a significant PE fraction and a non-significant PS fraction, the metacommunity is driven by species-sorting mechanisms. In this scenario, differences in communities relate to the presence of environmental gradients and the ability of species to exhibit a movement response to track these gradients. When the variance is decomposed into both significant PE and PS fractions then species-sorting and mass-effects processes will operate. Cottenie (2005) and Leibold et al. (2004) pointed out that mass-effects incorporate a spatial component generated by immigration and emigration dispersal events, in which species face a competition/dispersal trade-off (i.e. individuals can avoid competitive exclusion by immigrating into areas where they are good competitors). This pattern is therefore the result of a purely spatial signal which is independent on environmental conditions (Cottenie 2005). In a system that is completely devoid of a significant PE component and only consists of a PS component, neutral model processes (Hubbell 2001) will operate such that, because species and habitat are assumed to be similar, only dispersal processes will generate spatial patterns (Cottenie 2005).

Following this reasoning, my results suggest that species-sorting was the dominant process operating on the waterbird metacommunity in the April 2013 sampling period, while a combination of species-sorting and dispersal processes (incorporated into mass-effects) was dominant throughout the rest of the study period. In accordance with my findings, the results

of the meta-analysis revealed that species-sorting was a dominant mechanism operating across a wide range of taxa and ecological systems. This result does not, however, negate spatial dispersal processes which also play a role. Indeed the next most prevalent metacommunity type stemmed from a combination of species-sorting and mass-effects, which is what my results suggest through the majority of my sampling periods. Interestingly, the large SSE fraction in my study opposed the findings of Cottenie (2005), in which this component ranked lowest in explaining community variation. The SSE fraction is caused by induced spatial dependence which strengthens the importance of environmental component. This discrepancy between my findings and those of Cottenie (2005) could be due to three limiting factors of the meta-analysis. First, Cottenie (2005) used third-order polynomials of geographic coordinates to model the spatial component, which have been shown to be inferior to the newer MEM methods (Dray et al. 2006, 2012) that are able to model spatial variation at multiple scales. This could possibly have lead to a failure to adequately detect spatial patterns and hence downplay the role of spatial processes. Second, the data were obtained from studies conducted in northern temperate regions, which limits the ability to make general inferences for processes operating in tropical regions, such as my study site. Third, very few of the study systems included birds as the focal study organisms (the majority of studies focussed on macroinvertebrates and zooplankton). However, findings of other studies of avian metacommunities generally do support the species-sorting mechanisms as a dominant force (Barbaro et al. 2007, Meynard and Quinn 2008, Sattler et al. 2010, Gianuca et al. 2013, Özkan et al. 2013, Bonthoux and Balent 2015), although some studies do report either a lack of stable metacommunity processes (Driscoll and Lindenmayer 2009) or evidence of neutral dynamics (White and Hurlbert 2010, Meynard et al. 2011). These findings highlight the importance of explicitly incorporating spatial dynamics into community ecology research, instead of treating spatial autocorrelation as a nuisance component (Levin 1992, Dray et al. 2012).

The role of temporal variation in community processes has not been widely explored (but see Eros et al. (2012)), with the majority of findings resulting from either one or a couple of sampling periods. My study design allowed me to incorporate a temporal aspect that revealed distinct seasonal patterns. The variation in the prominence of PE (winter) and PS (summer) indicated that seasonal dynamics of both species and the landscape need to be understood to gain a deeper understanding of the temporally stable components structuring metacommunities. The change in importance of variance partitioning components could be

due to two factors. First, the majority of precipitation occurs in the summer months which coincide with the breeding period of resident waterbirds (Hockey et al. 2005). This results in a change in configuration of wetlands, with the availability of small ephemeral wetlands, often used by breeding waterbirds, greatly increased. A greater PS weighting might be related to the dispersal of waterbirds which are seeking out suitable breeding habitats and territories. This might strengthen the effect of inter-specific competition which would, in turn, alter local population dynamics (Holyoak et al. 2005, Gotelli et al. 2010). Second, the concurrent influx of non-breeding Palearctic migrant waterbirds during summer may also serve to amplify this spatial signal. In a temporal study on the metacommunity dynamics of stream fishes in Hungary, Eros et al. (2012) also found substantial variation in the relative contribution of PS, PE and SSE to total explained variance. This pattern could be attributed to changes in hydrology and water chemistry, which can act at fine temporal scales in river systems.

Another interesting aspect of our findings is the disparity between total explained variance in the waterbird metacommunity in the June 2012 sampling period compared to June 2013. Although the proportions of space-environment components remained similar, the total variance explained throughout my study was the highest in June 2012 (24.7%) and lowest in June 2013 (15.4%). This may be in part a result of the highly dynamic landscape of my study site, in which rainfall and wetland distributions exhibit high spatiotemporal variation. As proposed by Eros et al. (2012), there is a need to analyse data from multiple sampling periods to understand the structuring forces that contribute to variance in apparent metacommunity processes. A single snapshot of community organisation may hinder the ability to develop rigorous predictive models and conservation plans surrounding metacommunities. This point has recently received attention and Legendre and Gauthier (2014) have proposed methods to extend the application of spatially explicit statistical frameworks to those which incorporate temporal patterns (e.g. extension of eigenvector methods, such as MEMs, to analyse multivariate time-series data).

In addressing the second question, the results of the forward stepwise selection showed that vegetation structure variables contributed the highest relative R^2_{adj} to the portion of purely environmental component in the variance partitioning procedure with an average 44% across the seven sampling periods. This contribution was relatively stable through sampling periods. The proportion of aquatic surface and emergent vegetation was a variable that was most often selected (all sampling periods except October 2012) and had an average R^2_{adj} of 28%. Water quality variables were the next most important explanatory variables,

particularly salinity, which had an average R^2_{adj} of 21%. Rainfall variables were more important during the summer months, while land cover variables were more often selected in the winter months. Apart from vegetation structure, the contribution from the remaining three environmental variable groups showed marked variation through sampling periods. It is reasonable to expect this for rainfall and water quality, both of which can be driven by dynamics operating at fine temporal scales. It was, therefore, surprising that land cover (in which measurements did not change throughout the sampling period) showed a similar dynamic. Indeed none of the land cover variables were selected in either the December 2012 or February 2013 sampling periods. The proportion of emergent and surface vegetation and salinity were two variables that were particularly important in contributing to variance explained by the environmental component. The wetland clusters of False Bay, Eastern Shores and Western shores form part of Lake St Lucia, which is an estuarine system with high salinity levels. Most of the sites within these clusters had a low proportion of emergent and floating vegetation. In contrast sites within the Pongola floodplain and Muzi pan clusters had high proportions of surface vegetation and had water with low salinity levels (Tables 2.3 to 2.6, Chapter 2). On this basis the two variables played an important role because of their ability to discriminate between wetlands with opposing characteristics and waterbird assemblages (see the results of Chapter 5; different waterbird functional traits are filtered by environmental variables).

There are inherent limitations in my study that bear mentioning. First, the potential weakness of using variance partitioning to detect and differentiate between metacommunity processes has been pointed out (Smith and Lundholm 2010). Nevertheless, it is currently still one of the most powerful and frequently used methods. Second, Chang et al. (2013) showed that the conclusions drawn about metacommunities can depend heavily on the choice of environmental variables included in the analysis. The presence of a high PS or SSE fraction, as found in my study, may be the result of unmeasured spatially structured variables. However, the relationships between variables included in this analysis and waterbirds are well established – for example, for water quality (Halse et al. 1993, Kalejta-Summers et al. 2001b, Ashkenazi 2001, Cumming et al. 2013), vegetation structure (Murkin et al. 1997, Raeside et al. 2007, Russell et al. 2009) and rainfall (Roshier et al. 2002, 2008b, Kingsford et al. 2010). While it is nearly impossible to include all environmental variables relevant in the niche dynamics of a study organism, the choice of variables here is appropriate for addressing metacommunity hypotheses. The total explained variance in our sampling periods was

moderate; these values were on par with, and in some instances higher, than those in other similar studies (Sattler et al. 2010). Unexplained variation could be attributed to stochastic processes (e.g. increase in anthropogenic disturbance at a particular site) influencing our study system, but despite the high variance in spatiotemporal dynamics of wetlands in the southern African landscape coupled with the high mobility of waterbirds, this value was not excessively high.

This is the first study to investigate waterbird metacommunity dynamics across a large network of wetlands and thus makes a novel contribution to understanding how freshwater avian assemblages are structured. Species-sorting and mass-effect dynamics appear to be the dominant and most important drivers of community structure in waterbirds. Our findings regarding the relevance of spatial components do however suggest that niche dynamics do not operate in isolation. My results also highlight the utility of analysing metacommunity dynamics in multiple sampling periods and have shown the relative importance of spatial and environmental processes can vary significantly through time. Most importantly, this study serves to reiterate the importance of taking into account the spatial structure of organism communities.

6.6 Appendices

Appendix 1 List of the 53 waterbird species included in the metacommunity analysis.

Common name	Latin name
Common Sandpiper	*Actitis hypoleucos*
African Jacana	*Actophilornis africanus*
Malachite Kingfisher	*Alcedo cristata*
Egyptian Goose	*Alopochen aegyptiaca*
Black Crake	*Amaurornis flavirostris*
Hottentot Teal	*Anas hottentota*
Red-billed Teal	*Anas erythrorhyncha*
Cape Shoveler	*Anas smithii*
Yellow-billed Duck	*Anas undulata*
African Darter	*Anhinga rufa*
Grey Heron	*Ardea cinerea*
Goliath Heron	*Ardea goliath*
Purple Heron	*Ardea purpurea*
Squacco Heron	*Ardeola ralloides*
Cattle Egret	*Bubulcus ibis*
Water thick-knee	*Burhinus vermiculatus*
Curlew Sandpiper	*Calidris ferruginea*
Little Stint	*Calidris minuta*
Pied Kingfisher	*Ceryle rudis*
White-fronted Plover	*Charadrius marginatus*
Kittlitzs Plover	*Charadrius pecuarius*
Three-banded Plover	*Charadrius tricollaris*
Whiskered Tern	*Chlidonias hybrida*
White-winged Tern	*Chlidonias leucopterus*

White-faced Duck	*Dendrocygna viduata*
Great Egret	*Egretta alba*
Little Egret	*Egretta garzetta*
Yellow-billed Egret	*Egretta intermedia*
Red-knobbed Coot	*Fulica cristata*
Common Moorhen	*Gallinula chloropus*
African Fish-Eagle	*Haliaeetus vocifer*
Black-winged Stilt	*Himantopus himantopus*
Grey-headed Gull	*Larus cirrocephalus*
Yellow-billed Stork	*Mycteria ibis*
African Pygmy-Goose	*Nettapus auritus*
Great White Pelican	*Pelecanus onocrotalus*
Pink-backed Pelican	*Pelecanus rufescens*
Reed Cormorant	*Phalacrocorax africanus*
White-breasted Cormorant	*Phalacrocorax carbo*
Ruff	*Philomachus pugnax*
Greater Flamingo	*Phoenicopterus ruber*
African Spoonbill	*Platalea alba*
Spur winged Goose	*Plectropterus gambensis*
Glossy Ibis	*Plegadis falcinellus*
African Purple Swamphen	*Porphyrio madagascariensis*
Caspian Tern	*Sterna caspia*
Little Grebe	*Tachybaptus ruficollis*
White-backed Duck	*Thalassornis leuconotus*
African Sacred Ibis	*Threskiornis aethiopicus*
Wood Sandpiper	*Tringa glareola*
Common Greenshank	*Tringa nebularia*
Blacksmith Lapwing	*Vanellus armatus*
African Wattled Lapwing	*Vanellus senegallus*

Appendix 2 Results of the data-driven approach for selecting the most suitable spatial weighting matrix for creation of MEM variables. dnn, distance-based criterion; del, Delaunay triangulation; gab, Gabriel graph; rel, relative neighbourhood graph; mst, minimum spanning tree; bin, binary; f1, linear function; f2, concave-down function; f3, concave-up function. The units of the γ parameter are in km. The values of α and β are one of nine integers ranging from 2 to 10. Results are shown separately for each sampling period: April 2012 (Appendix 2.1), June 2012 (Appendix 2.2), October 2012 (Appendix 2.3), December 2012 (Appendix 2.4), February 2013 (Appendix 2.5), April 2013 (Appendix 2.6) and June 2013 (Appendix 2.7).

Appendix 2.1

Connectivity	Weighting function	AICc	Parameter values
dnn	f2	-18.99	α = 6; γ = 36.84
dnn	bin	-18.83	γ = 30.18
dnn	f3	-18.20	β = 2; γ = 36.90
dnn	f1	-17.79	γ = 39.15
del	f1	-17.74	
gab	f1	-17.65	
del	f3	-17.55	β = 2
mst	f1	-17.43	
del	bin	-17.32	
gab	f2	-17.29	α = 2
mst	f2	-17.28	α = 8
rel	f3	-17.27	β = 2
mst	f3	-17.27	β = 2
gab	f3	-17.26	β = 2
rel	f2	-17.24	α = 3
del	f2	-17.20	α = 5
rel	f1	-16.88	
gab	bin	-16.77	
mst	bin	-16.55	
rel	bin	-16.49	

Appendix 2.2

Connectivity	Weighting function	AICc	Parameter values
dnn	f2	-21.14	$\alpha = 2; \gamma = 45.32$
dnn	f1	-20.43	$\gamma = 48.43$
gab	f3	-19.45	$\beta = 2$
dnn	f3	-19.44	$\beta = 2; \gamma = 39.15$
del	f3	-19.41	$\beta = 2$
dnn	bin	-19.35	$\gamma = 42.24$
mst	f1	-19.27	
rel	f3	-19.16	$\beta = 2$
mst	f3	-19.16	$\beta = 2$
del	f1	-18.94	
mst	f2	-18.91	$\alpha = 2$
rel	f1	-18.83	
rel	f2	-18.78	$\alpha = 2$
gab	f1	-18.76	
rel	bin	-18.51	
del	f2	-18.28	$\alpha = 2$
mst	bin	-18.03	
gab	f2	-17.92	$\alpha = 2$
del	bin	-17.59	
gab	bin	-17.18	

Appendix 2.3

Connectivity	Weighting function	AICc	Parameter values
dnn	bin	-19.24	$\gamma = 32.42$
dnn	f2	-19.23	$\alpha = 7; \gamma = 31.27$
gab	bin	-18.32	
dnn	f1	-18.29	$\gamma = 39.15$
del	f1	-18.18	
gab	f1	-18.13	
mst	f1	-18.01	
gab	f2	-17.95	$\alpha = 3$
rel	f3	-17.84	$\beta = 2$
mst	f3	-17.84	$\beta = 2$
del	f2	-17.81	$\alpha = 2$
mst	f2	-17.81	$\alpha = 10$
dnn	f3	-17.79	$\beta = 2; \gamma = 29.06$
del	bin	-17.75	
rel	f1	-17.75	
rel	bin	-17.69	
mst	bin	-17.67	
rel	f2	-17.65	$\alpha = 10$
gab	f3	-17.62	$\beta = 6$
del	f3	-17.61	$\beta = 2$

Appendix 2.4

Connectivity	Weighting function	AICc	Parameter values
dnn	f1	-17.44	$\gamma = 44.30$
dnn	f2	-17.38	$\alpha = 2; \gamma = 44.17$
dnn	f3	-16.81	$\beta = 3; \gamma = 39.15$
gab	f1	-16.69	
rel	f3	-16.67	$\beta = 2$
mst	f3	-16.67	$\beta = 2$
del	f3	-16.66	$\beta = 3$
gab	f3	-16.56	$\beta = 3$
rel	f2	-16.46	$\alpha = 2$
dnn	bin	-16.44	$\gamma = 47.40$
mst	f1	-16.39	
mst	f2	-16.31	$\alpha = 3$
gab	f2	-16.26	$\alpha = 2$
del	bin	-16.07	
gab	bin	-16.03	
rel	f1	-16.01	
rel	bin	-15.98	
del	f2	-15.85	$\alpha = 9$
mst	bin	-15.82	
del	f1	-15.73	

Appendix 2.5

Connectivity	Weighting function	AICc	Parameter values
dnn	f2	-17.93	$\alpha = 4; \gamma = 31.24$
dnn	f1	-17.43	$\gamma = 34.66$
mst	f2	-17.20	$\alpha = 3$
dnn	bin	-17.14	$\gamma = 31.30$
rel	bin	-16.95	
rel	f2	-16.75	$\alpha = 2$
mst	f1	-16.42	
rel	f1	-16.34	
mst	bin	-16.32	
gab	f1	-16.27	
gab	bin	-15.92	
gab	f2	-15.87	$\alpha = 2$
del	f3	-15.84	$\beta = 2$
del	bin	-15.80	
dnn	f3	-15.78	$\beta = 2; \gamma = 36.90$
rel	f3	-15.65	$\beta = 2$
mst	f3	-15.65	$\beta = 2$
del	f1	-15.60	
gab	f3	-15.56	$\beta = 2$
del	f2	-15.49	$\alpha = 5$

Appendix 2.6

Connectivity	Weighting function	AICc	Parameter values
dnn	f2	-16.76	$\alpha = 3; \gamma = 39.15$
dnn	f1	-16.54	$\gamma = 47.40$
dnn	f3	-15.57	$\beta = 2; \gamma = 40.18$
del	f3	-15.50	$\beta = 2$
rel	f3	-15.39	$\beta = 2$
mst	f3	-15.39	$\beta = 2$
gab	f3	-15.37	$\beta = 2$
dnn	bin	-15.36	$\gamma = 43.27$
mst	f1	-15.34	
rel	bin	-15.18	
mst	f2	-15.13	$\alpha = 7$
rel	f2	-15.11	$\alpha = 5$
del	f1	-15.10	
del	f2	-15.06	$\alpha = 2$
mst	bin	-14.97	
del	bin	-14.96	
gab	f1	-14.95	
gab	bin	-14.88	
gab	f2	-14.81	$\alpha = 10$
rel	f1	-14.75	

Appendix 2.7

Connectivity	Weighting function	AICc	Parameter values
dnn	f2	-17.46	$\alpha = 2; \gamma = 40.18$
dnn	f1	-17.05	$\gamma = 48.43$
mst	f1	-16.77	
mst	f2	-16.23	$\alpha = 2$
gab	f1	-16.19	
gab	f2	-16.08	$\alpha = 2$
rel	f1	-15.95	
del	f3	-15.92	$\beta = 2$
dnn	bin	-15.81	
rel	f3	-15.75	$\beta = 2$
mst	f3	-15.75	$\beta = 2$
del	bin	-15.73	
gab	f3	-15.71	$\beta = 2$
rel	f2	-15.69	$\alpha = 2$
gab	bin	-15.67	
del	f1	-15.65	
del	f2	-15.62	$\alpha = 2$
mst	bin	-15.50	
dnn	f3	-15.46	$\beta = 2; \gamma = 39.15$
rel	bin	-15.04	

7 SYNTHESIS

7.1 Introduction

In a time when anthropogenic activities are having an increasingly negative impact on species and the habitats in which they live, it is vital that we acquire an intimate knowledge of the factors which precipitate and structure animal movement. This will provide a basis from which to understand and predict animals' responses to the deleterious effects of processes such as habitat alteration, habitat fragmentation and climate change. In addition to enriching our theoretical understanding, advances in movement ecology have important implications for applied conservation strategies. For instance, understanding the mechanisms behind the movement of invasive species can aid in the management and control of further spread. While there are a myriad of studies focussing on discrete aspects of animal movement, there is now a pressing need to illuminate generalities in movement phenomena (Holyoak et al. 2008, Nathan et al. 2008). The movement ecology framework (Fig. 1.1) provides in part, an integrated method for achieving this goal. A fundamental challenge lies in understanding how the various components affect the movement of the organism in question.

The extent of our understanding of the movement ecology of waterbirds in arid environments is limited. This is especially true in southern Africa, given that a significant proportion of arid zone studies have been conducted in Australia (Kingsford and Norman 2002, Roshier et al. 2008b, Kingsford et al. 2010). Unlike highly seasonal temperate environments, patchily distributed resources relevant for waterbirds are characterised by high levels of spatiotemporal variability. In response to this, many waterbird species have adopted nomadic movement strategies which appear largely unpredictable. The number of movement-focussed studies has steadily increased in the last decade; however, on the whole, nomadism as a movement phenomenon has been poorly studied. In a review of movement ecology research, Holyoak et al. (2008) found that only 0.8% of studies used the term "nomadism"; the most frequently used terms were "migration" and "dispersal". In an effort to address these issues, I explored the mechanisms driving the movement of waterbirds using a two-tiered approach, relating respectively to individuals and communities. I aimed to go beyond an

observation or correlative approach by modelling movements in a more mechanistic manner. In the first part of my study, I placed emphasis on understanding the role of external factors on individual waterfowl movement, while also touching on aspects of navigational capacity and internal state. In the second part of my study, I explored how movement operates to structure and maintain waterbird communities.

7.2 Summary of findings

Using point-based telemetry data of Egyptian Geese, I explored habitat selection and functional responses in a predation-forage quality trade-off at the home range scale (Chapter 3). I found little support for the role of internal factors (in the form of life stage) in explaining variation in habitat selection of geese. Instead, variation in the resource selection functions was best modelled by external landscape factors, specifically of differences in rainfall season and study site. My results showed that agricultural areas and wetlands were two of the more important habitats used by geese. Geese altered the magnitude of their selection in the two habitats seasonally to adjust to changes in productivity and distribution of resources. Interestingly, individuals from two distant populations exhibited remarkably consistent patterns of selection across seasons and habitats, although the actual magnitude of selection differed. Coupled with the finding that individuals contributed a small fraction of variance to the models suggests that Egyptian Geese are making similar decisions of habitat use at the home range scale. This was surprising and contrasted with other studies which have highlighted the role of individual variation in explaining movement patterns within arid landscapes (Roshier et al. 2008b, Oppel et al. 2009).

Using a functional response approach, I then examined trade-offs between minimising the risk of predation and access to high quality forage. This is a question that has been explored widely in large ungulates (Benhaiem et al. 2008, Godvik et al. 2009, Hansen et al. 2009, Herfindal et al. 2009), and the results can be used to assess whether predation risk or forage quality is a limiting factor at the home-range scale (Mysterud and Ims 1998). This was, however, the first time this trade-off has been addressed in a herbivorous waterbird. In both seasons Egyptian Geese showed functional responses in wetland (providing greater safety) and agricultural habitats (providing greater forage quality). This was contrary to my expectation that functional responses would occur in one, but not both, of these habitats. Safety from predators and access to high quality of resources could both possibly be limiting

factors that drive movements at the home range scale for Egyptian Geese (Cumming et al. 2016).

In the remaining section, aimed at understanding the drivers of waterbird movement from an individual perspective, I sought to identify the key environmental landscape variables (measured with remote sensing techniques) that influence movements of Red-billed Teal and Egyptian Geese (Chapter 4). Using trajectory-based telemetry data within the first-passage time movement model, I identified these variables and tested two competing movement hypotheses: "reactive" and "prescient". Primary productivity and precipitation were identified as the important landscape variables that drove movement in both species. My results showed support for the prescient movement hypothesis in geese and teal - waterfowl were able to detect and respond to shifts in resource conditions in a given area based on changes in the magnitude and direction of changes within a habitat patch prior to arrival. Egyptian Geese were shown to have responded to increases in food quality in a similar manner to that of herbivorous waterfowl in the northern hemisphere (Green Wave Hypothesis; van der Graaf et al. (2006), Shariatinajafabadi et al. (2014)). Red-Billed Teal responded in a contrasting manner; their movements were partly a response to decreasing primary productivity. I attributed this pattern to the ability of teal to capitalise on nutritious food sources such as grass seeds (which are more abundant after the peak growing season). Having spatial awareness would allow waterfowl to capitalise on favourable habitat conditions and leave areas when quality starts to decline, providing an adaptive advantage through periods of resource uncertainty. Indeed, the role of spatial memory has received renewed attention as of late (Mueller and Fagan 2008a, Van Moorter et al. 2009, Fagan et al. 2013). In a recent home range study, Seidel and Boyce (2015) showed that Elk *Cervus elaphus* made directed movements back to patches that had been previously identified as containing high quality forage. This was the first application of the first-passage time movement model to waterfowl and my results suggest prior knowledge, and possibly memory, of the landscape may be particularly relevant to birds in arid landscapes. I have also shown that movements are a set of complex behaviours and waterfowl appear not to be merely making random walks through the landscape and ceasing movement when suitable resources are encountered.

In the section of my thesis aimed at understanding movement in waterbirds from a community perspective, I first sought to explore how environmental characteristics in the landscape filter functional traits of waterbirds, and also if birds with different traits occupy

distinct ecological niches (Chapter 5). The multivariate functional trait approach allowed me to evaluate relationships between several traits and environmental variables. I showed that there were several significant relationships between functional traits and environmental characteristics. Waterbirds with greater movement ability (nomads and inter-African migrants) responded to variation in broad-scale landscape variables, suggesting a strong link between the scales that resources are structured and distributed, and the movement capabilities of waterbirds. In accordance with previous findings, my results also highlighted several strong associations between vegetation structure and foraging habitat traits, which suggests that vegetation structure is a particularly important driver for the distribution of several waterbird species (Murkin et al. 1997, Russell et al. 2009, Terörde and Turpie 2013). There was a clear separation of movement traits in multivariate space that formed a gradient of movement ability from low (resident species and local movers) through to medium (intra-African migrants and nomads) and ending with high ability (inter-African migrants). By considering foraging habitat and dietary traits in conjunction with movement, there was further evidence for niche separation: inter-African migrants fed on invertebrate in short vegetation and mudflats; nomads and intra-African migrants foraged in both shallow and deep water; and residents and local movers had a carnivorous diet. My results suggested that movement capacity can serve as a mechanism which allows waterbirds to integrate differently over landscape variability, which itself can drive differences in the use of ecological niches. More mobile birds were able to exploit resources on broader scales than less mobile birds. Using a functional trait approach to combine movement traits with foraging habitat and dietary group allowed me to conclude that movement plays a key role in how waterbirds exploit different ecological niches.

Following on from the first community-focused analysis, I then explored the metacommunity processes that structured waterbird communities using a variance partitioning approach (Chapter 6). This allowed me to assess the relative importance of spatial and environment processes and in doing so tested four metacommunity paradigms: species sorting, mass effects, patch dynamics and neutral models. Purely spatial, purely environmental and spatially structured environmental components all contributed significantly to the overall explained variance in waterbird beta-diversity. The relative strength of these components did however change through the sampling periods. Of the pure fractions, environmental factors were more dominant in the winter months, while spatial processes were higher in the summer months. Overall, species-sorting mechanisms appear to

be the dominant metacommunity process. While there is only one other example of a waterbird metacommunity study (Gianuca et al. 2013), findings from other systems do show that species sorting mechanisms are the dominant processes operating across a wide variety of taxa (Cottenie 2005). However, the presence of a significant spatial component does suggest that niche dynamics do not operate in isolation and that dispersal processes contribute to the observed patterns in beta-diversity. Incorporating multiple sampling periods allowed me to illustrate distinct seasonal patterns in metacommunities. To more fully understand how communities are structured, and how movement between communities varies, it is therefore essential to analyse data from multiple sampling events. My results also suggest that even in systems that lack significant barriers to dispersal, spatial processes do indeed operate.

7.3 Future directions

Using telemetry data I was able to detect and test mechanisms driving observed movement patterns of waterbirds. These data were based on one GPS fix every 2 and 4 h for Egyptian Geese and Red-billed Teal respectively. The spatial accuracy of fixes (relocations) in our data was ~20 m, which can be considered very high (Cumming and Ndlovu 2011). However, because of the size of solar-powered GPS transmitters and associated battery constraints, the daily fix-rate was fairly low and missed fixes resulted in days that consisted of between one and three fixes. While these data have proved useful for detecting patterns of habitat use and movement, exploring fine scale behaviour and movement was not possible. Behaviour of an individual animal is primarily characterised by the presence or absence of movement. The advent of devices such as tri-axial accelerometers has allowed researchers to gain insight into fine scale behaviour in animals (Wilson et al. 2008). This is particularly useful for identifying habitats and environments in which behaviours such as resting or foraging occur. For instance, accelerometers attached to cormorants have enabled the researchers to identify precisely where activities such as flying, diving and resting occurred (Laich et al. 2008, Shepard et al. 2010), as well as understanding locomotion strategies (Kato et al. 2006). Accelerometer devices have been largely been applied to marine birds and mammals (Wilson et al. 2008), in part because these animals are often central-place foragers or nesting individuals which allows for effective retrieval of devices. While retrieval of devices from free ranging waterfowl presents a huge barrier to the use of such technology, insights gained from such data would be invaluable. Access to this form of data would allow us to address

questions such as: at what time of day do waterfowl actively forage; which habitats are used for loafing and comfort related activities; do waterfowl change feeding mode (e.g. grazing, upending or dabbling) in specific wetlands; and how do aggressive interactions with conspecifics affect habitat use? All of this information would complement our understanding of broad scale movements to further address components of the movement ecology framework (e.g. the internal state of the focal individual).

Habitats, and their abiotic and biotic components, are structured at multiple spatial and temporal scales (Wiens 1989, Levin 1992). Understanding how animals respond to this heterogeneity requires studies that examine movement behaviour not only in an individual's local environment, but also from broader scales, such as a species' biogeographical range. Depending on the species and habitats considered, the strength of many ecological processes can show significant variation. For instance, because studies are often limited to small geographical extents and short temporal periods, the predominance of top-down and bottom-up processes has not been adequately resolved (Gripenberg and Roslin 2007). Therefore, to further develop our theoretical understanding of movement, it is necessary to seek approaches that integrate findings based on movement data collected from individuals with those collected from communities, measuring variation in abundance and composition over long temporal periods.

Focussing on the movement of an individual is limiting when one seeks to understand processes that structure movement at slower rates over longer time scales (e.g., decadal or evolutionary) and occur at higher levels of hierarchical organisation (e.g., metacommunities). There is a need for landscape-level studies that track how populations and communities respond to environmental variability while simultaneously monitoring individual level movement responses. This would allow for an integration of theories surrounding how individual choices are embedded within processes important for the dynamic structuring of communities (e.g., inter- and intraspecific competition, colonisation, emigration, and predation). In a similar manner, theories surrounding community dynamics could be framed in a manner which acknowledges the constraints that community organisation processes impose on the internal components of individual movement. However, investigating the causes and mechanisms of individual movement is a necessary first step and starting point for addressing processes that shape population, community and ecosystem dynamics. There is, for instance, a clear link between the internal state component of the

movement ecology framework and evolutionary consequences of movement, given that the motivation to move is driven by individual fitness benefits (Nathan et al. 2008).

Communities are made up of multiple species which may differ in both their movement ability and their response to similar changes in local environmental dynamics. A potential issue for understanding how individual movement responses feed into broader community dynamics stems from apparently similar species employing divergent movement strategies. This may cause difficulties when attempting to disentangle structuring forces within broader communities. Functional traits of movement could provide a productive avenue for overcoming this issue. If we can identify the proximate drivers of movement from multi-species individual level studies, assuming a wide variety of traits are incorporated, it should be possible to extrapolate those general findings to explain community patterns from a functional instead of species perspective.

There are cases where extending the conceptual movement ecology framework to understand processes at higher organisational levels have proved to be a productive endeavour. Damschen et al. (2008) modified the movement ecology framework to explore the dynamics of species richness in bird and wind dispersed species within fragmented plant communities. In a study of Iberian Lynx *Lynx pardinus*, Revilla and Wiegand (2008) examined movement behaviour of individuals between patches to demonstrate how these movements affected demographic rates and metapopulation dynamics. In a comprehensive case of developing a theoretical framework, Jeltsch et al. (2013) extended the movement ecology model to up-scale individual movement and include concepts of individuals as mobile links (of functions, resources and genes between communities) and coexistence mechanisms (stabilising and equalising). The primary goal was to integrate these components to further enrich the understanding of how the movement of organisms shapes biodiversity patterns across multiple spatiotemporal scales (Jeltsch et al. 2013). These cases demonstrate how theories of individual level movement and community patterns can be effectively combined to create a comprehensive and inclusive framework.

7.4 Conclusions

Waterbirds in arid environments face a different set of constraints than their northern-hemisphere counterparts, specifically with respect to the predictability of environmental resources. In southern Africa, rainfall plays a significant role in determining the availability

and extent of wetland resources. This constraint has prompted unpredictable and often extensive nomadic movement patterns. Movement in southern African waterbirds is a complex strategy, and I have shown that having a spatial awareness and prior knowledge of the landscape is an important characteristic allowing waterbirds to exploit patchily distributed resources. In many cases the movement and models and analytical techniques used in my study have not previously been applied to waterbird individuals and communities. This thesis makes a significant contribution to our understanding of both the movement ecology of southern African waterbirds, and mechanisms by which waterbirds make movement decisions in landscapes characterised by unpredictable changes in resource distributions. By combining telemetry data with remote sensing data, I was able to address a fundamental question of the environmental drivers of movement (Fryxell et al. 2008, Getz and Saltz 2008, Avgar et al. 2013). Exploring the movement of individuals over broad spatial and temporal scales, as well as analysing waterbird community data, allowed me to adopt a multi-scale approach to understanding movements. In doing so I addressed not only components of the movement ecology framework, but also the processes that structure metacommunities and ecological niches of waterbirds.

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